

BREEDING ECOLOGY OF WHIMBRELS (*NUMENIUS PHAEOPUS*)
IN INTERIOR ALASKA

By

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Abstract

Whimbrels *Numenius phaeopus* breed in tundra-like habitats, both beyond treeline and within the boreal forest of interior Alaska. Despite their widespread distribution and designation as a species of conservation concern, their ecology has been particularly understudied in Alaska. During 2008–2012, I initiated the first dedicated study of Whimbrel breeding ecology in Alaska, and the first such study of any boreal-breeding shorebird in the state. Within a habitat mosaic of forest, woodlands, muskeg, scrub, and ponds within the floodplain of the Kanuti River in north-central Alaska, Whimbrels bred in the three largest (of nine) patches of discontinuous tussock tundra. These Whimbrels exhibited a compressed annual breeding schedule with the first birds arriving about 6 May and nests hatching about 17 June. Evidence for clustered and synchronous nesting, which may aid in predator defense, was equivocal. Most (69%) Whimbrels nested in mixed shrub-sedge tussock bog. I modeled nest-site selection at multiple spatial scales for 39 nests; however, the only variables important in the models were at the finest scale around the nest, namely that nests tended to be located on hummocks and exhibited lateral cover. Model results for nest survival of 67 nests over 4 years revealed a considerable difference in nest success (92% vs. 41%) at the two largest patches studied; this site effect was largely unexplained.

To investigate Whimbrel ecology more broadly in the boreal biome, in 2013 I designed and conducted a Whimbrel-specific survey comprising 279 point counts within 28 transects along the road system of interior Alaska. I detected Whimbrels on just 32% of transects and 11% of count points. Although I detected Whimbrels at 3 sites where they had not been reported previously, I failed to detect them at several historically occupied sites. Dwarf shrub meadow was the most

commonly observed habitat for all points visited. I modeled Whimbrel presence based on coarse habitat and avifaunal community features; no models were well supported.

Between the local and regional surveys, my results tended to reinforce several widespread, but not necessarily investigated, descriptions about the breeding ecology of Whimbrels. My studies supported the premises that Whimbrels are patchily distributed on the landscape and often breed in clusters. Breeding of individuals and occupancy of some patches may be annually variable. Despite analyses of multiple habitat features at multiple spatial scales, I mostly observed a lack of specificity in where they bred among tundra-like patches, and where they nested specifically within such patches. This suggests that Whimbrels are tundra habitat generalists on their breeding grounds. Such phenotypic plasticity may be particularly adaptive in the dynamic, wildfire-prone landscape of interior Alaska.

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General Introduction

Most of the world's shorebirds (suborder Charadrii; del Hoyo *et al.* 1996), and nearly all sandpipers (family Scolopacidae), are highly migratory and breed at northern latitudes (Colwell 2010). Indeed the efforts of some curlews (*Numenius* spp.) and godwits (*Limosa* spp.), collectively composing the tribe Numeniini (i.e., numeniids), to reach their breeding grounds can be prodigious (Marks *et al.* 2002, Gill *et al.* 2005, Senner *et al.* 2014), yet the time in the shorebird's annual cycle spent on the breeding grounds is relatively short. For example, a successfully breeding female Whimbrel *N. phaeopus* may spend as little as 12% of her annual cycle on the breeding grounds in Alaska (Skeel & Mallory 1996, Chapter 1), despite having come from perhaps as far as southern Chile (Johnson *et al.* 2007, Andres *et al.* 2009).

Although a Whimbrel in Alaska may only spend 6 to 11 weeks engaged in breeding activity, there are a considerable number of decisions to make in the effort. First, Whimbrels need to decide where on the vast landscape they will breed. Male Whimbrels generally show high breeding site fidelity (citations in Skeel & Mallory 1996), whereas site fidelity in females appears linked to breeding success with some birds not returning to a site if they were unsuccessful the previous year (Skeel 1983). Whimbrels also must decide when to arrive, start defending a territory, and initiate courtship and nesting activities, including whether their activities should be synchronized with sympatrically breeding conspecifics and other species that can aid in nest and chick defense (e.g., predator-mobbing shorebirds; Sordahl 1981). The timing for these could be profoundly influenced by the amount of snow cover, timing of snow melt, and weather (Smith *et al.* 2010). Once a mated pair is established, nest-site selection must be

evaluated at multiple scales around the prospective nest. At a coarse scale, the habitat patch must have sufficient size and food resources to accommodate the feeding of not only the pair, but their offspring (Andren & Angelstam 1988). At a finer scale, habitat assessments may concern questions of openness, wetness, numbers and distribution of shrubs and trees, and microtopography (Pirie 2008, Ballantyne & Nol 2011). The pair must also assess how closely it will tolerate fellow nesting Whimbrels and other species. Such nest-site assessments are largely driven by predation, which for many shorebirds is the primary influence on breeding success (Colwell 2010). Indeed for Whimbrels in Churchill, Manitoba, Canada, predation has at times been the most important factor negatively affecting both hatching success (Jehl 1971) and nesting success (Skeel 1983).

As the world's most widespread numeniid, Whimbrels scattered across both the Palearctic and Nearctic (Cramp & Simmons 1983) have been making decisions for millennia about when, where, and with whom to breed. Two disjunct populations breed in North America (*N. p. hudsonicus*; American Ornithologists' Union 1998), the eastern located west and south of Hudson Bay, and western in Alaska and northwestern Canada (Skeel & Mallory 1996). However, like shorebird populations generally (Zöckler *et al.* 2003, Thomas *et al.* 2006) and numeniids especially (Stap 2009) throughout the world, North America's Whimbrel populations have been designated as of high conservation concern in both Canada (Donaldson *et al.* 2000) and the United States (USSCP 2004) and are reported to be declining overall (Andres *et al.* 2012). The U.S. Shorebird Conservation Plan Partnership (2015) formally recognized the western population (i.e., the proposed *N. p. rufiventris*; Engelmoer & Roselaar 1998) as 'shorebirds of conservation concern' requiring 'management attention' based primarily on population size and threats on the non-breeding grounds (B. Andres, unpubl. data). The

sensitivity of this designation is further supported more locally by the Alaska Shorebird Group (2008a) and Audubon Alaska (Kirchhoff & Padula 2010).

Despite the species' status, studies of its breeding ecology have been few and restricted in North America. The species has been relatively well studied on the breeding grounds in Churchill, Manitoba (Skeel 1983, Lin 1997, Ballantyne & Nol 2011, 2015) and at the Mackenzie River Delta, Northwest Territories (Dickson *et al.* 1989, Gratto-Trevor 1996, Pirie *et al.* 2009, Pirie & Johnston 2012). However, Whimbrels have been little studied in Alaska (but see McCaffery 1996, Neipert *et al.* 2014) even though an estimated 80% of the western population breed there (Alaska Shorebird Group 2008a). Indeed, despite the Whimbrel's widespread distribution and conspicuousness on its North American breeding grounds, there still exist important information gaps about its basic ecology (McCaffery 1996, Skeel & Mallory 1996, Wilke & Johnston-González 2010). Prominent parameters for which information is incomplete include: breeding distribution, abundance and densities, and factors affecting nest success, particularly for *N. p. rufiventris* (Skeel & Mallory 1996).

Whimbrels are suspected widespread but discontinuous breeders throughout Alaska's tundra and some taiga habitats (Gibson 2011, Gotthardt *et al.* 2013). Whereas tundra is generally common beyond treeline in western and northern Alaska, such habitat is more limited and patchily distributed in Alaska's boreal Interior, making access to Whimbrels challenging. Indeed the vastness of the Interior (composing some one-third of Alaska (Gibson 2011)), the complex mosaic of its habitats, and the relatively dispersed distribution of boreal-breeding shorebirds, have all contributed to severely limiting the study of Alaska's boreal shorebirds, including

Whimbrels, especially when compared to the rich ornithological history for shorebirds at the state's periphery (i.e., beyond treeline; Fig. 0.1; Alaska Shorebird Group 2008b, 2009, 2010, 2011, 2012). Many recent studies of Alaska's coastal shorebirds have explored the potential impacts of climate change (Rehfish & Crick 2003, Meltofte *et al.* 2007, Saalfeld *et al.* 2013, Liebezeit *et al.* 2014). Nevertheless, threats associated with climate change for the Interior are likewise serious, especially for limited habitats like boreal tundra and the shorebird populations that breed there. Advancing treeline (Lloyd 2005), wetland drying (Riordan *et al.* 2006, Roach *et al.* 2011), increased shrubification (Tape *et al.* 2006), peatland loss (Frolking *et al.* 2011), and more active fire regimes (Kasischke *et al.* 2010) are all hypothesized changes to Alaska's Interior and consequentially possible threats to its shorebirds.

In 2008 I began the first of six years of multi-week ornithological studies for Kanuti National Wildlife Refuge (Refuge) near the Kanuti River in north-central Alaska during which I discovered Whimbrels and Hudsonian Godwits *L. haemastica* breeding. As the interior Alaska representative to the Alaska Shorebird Group, I was familiar with the paucity of information on these two numeniids of high conservation concern, especially regarding their breeding ecology in boreal Alaska (Alaska Shorebird Group 2008a). A year later the breeding ecology of these Whimbrels became a major focus of study for me and the Refuge—addressing fundamental questions about timing, distribution (both locally and across interior Alaska), density, nest-site selection, nesting success, and the factors affecting these demographic parameters. It was also important to demonstrate the feasibility and need for studies on shorebirds breeding in the boreal biome. Indeed, this became the first study dedicated to Whimbrels breeding in Alaska, and the first for any breeding shorebird in the boreal interior of Alaska.

The overall goal of my research was to investigate the breeding ecology of Whimbrels in interior Alaska at multiple spatial and population scales. During 2008–2012, I described the nesting ecology of a small population of Whimbrels breeding in isolated tundra patches within north-central Alaska’s boreal forest (Chapter 1). I examined the timing of breeding from arrival through hatch, nesting distribution and density, habitat features and their influence on nest-site selection at three spatial scales, and the factors affecting nest survival. In light of projected threats to boreal environments, I explored factors that may limit Whimbrel distribution and reproductive success within the more patchily distributed breeding habitats of interior Alaska. Thus, having looked at breeding ecology at a local scale, I was then interested in how representative this population and study area were more broadly across interior Alaska. I designed and conducted a Whimbrel-specific survey to identify the presence, absence, and coarse habitat data for Whimbrels breeding along the highway system of interior Alaska (Chapter 2). I applied my results to an explanatory model designed to better guide future efforts to predict Whimbrel distribution beyond the Interior’s road corridors. Further, the survey would likely identify heretofore unknown ‘hot spots’ at which future local breeding studies could be conducted (like Chapter 1). Finally, during this multi-year intensive study, I incidentally observed behaviors and other natural history phenomena about Whimbrels not amenable to inclusion in Chapters 1 and 2. I have thus included descriptions about these observations in Chapter 3 and Appendices A and B.

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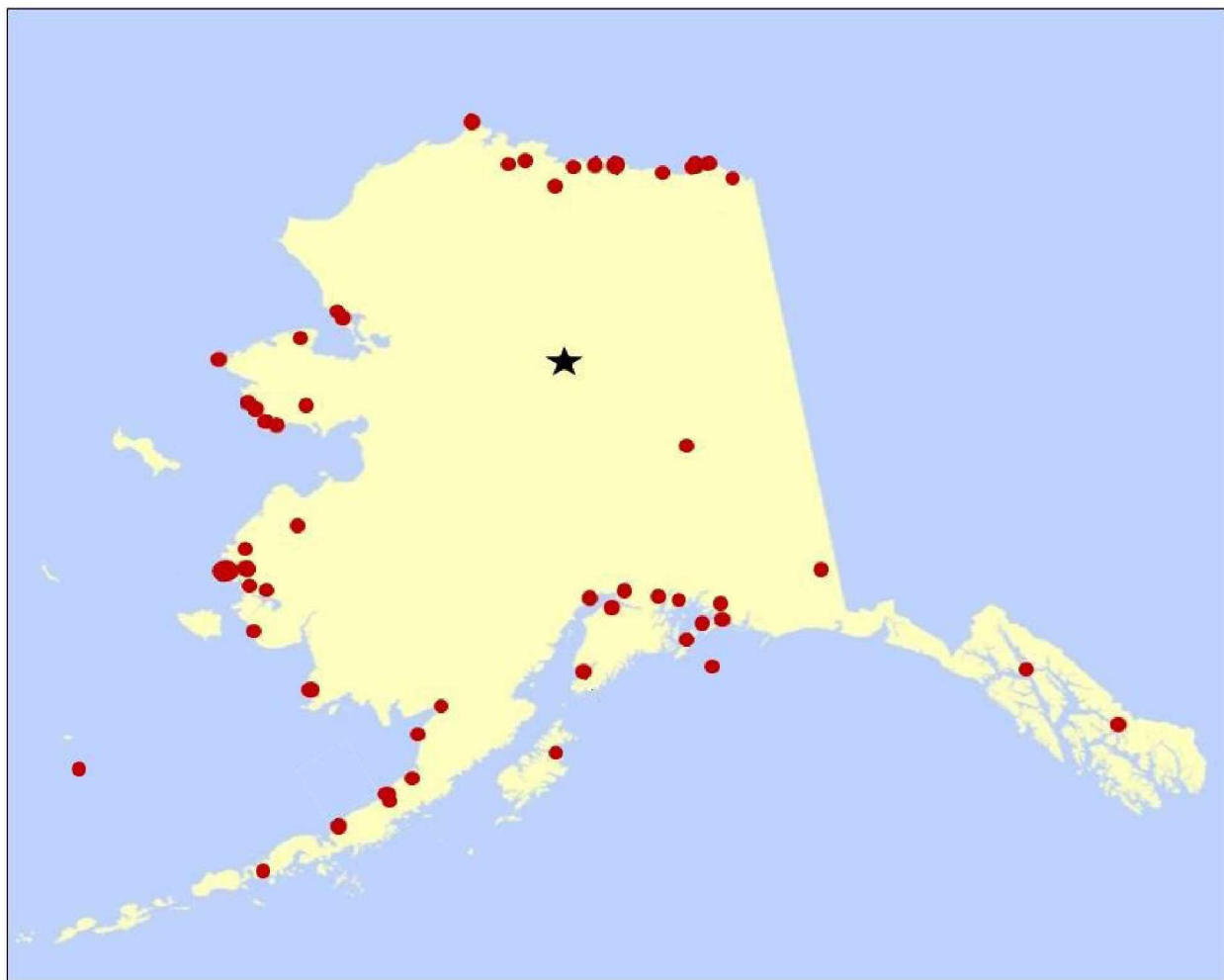


Fig. 0.1. Locations of shorebird studies in Alaska during 2008–2012 (combined figures from Alaska Shorebird Group 2008b, 2009, 2010, 2011, 2012). Multi-year study on Kanuti NWR is represented by the star in north-central Alaska.

Chapter 1. Nesting ecology of Whimbrels in boreal Alaska.¹

1.1 ABSTRACT

Breeding ecology studies of boreal waders have been relatively scarce in North America. This paucity is due in part to boreal habitats being difficult to access, and boreal waders being widely dispersed and thus difficult to monitor. Between 2008 and 2014 we studied the nesting ecology of Whimbrels *Numenius phaeopus hudsonicus* in interior Alaska, a region characterized by an active wildfire regime. Our objectives were to (1) describe the nesting ecology of Whimbrels in tundra patches within the boreal forest, (2) assess the influence of habitat features at multiple scales on nest-site selection, and (3) characterize factors affecting nest survival. Whimbrels nested in the largest patches and exhibited a consistently compressed annual breeding schedule. We hypothesized that these Whimbrels would exhibit synchronous and clustered nesting, but observed synchronous nesting in only 2009 and 2011, and evidence of clustered nesting at just one study area in 2009, providing limited support for the hypothesis. Nests tended to be on hummocks and exhibited lateral concealment around the bowl, suggesting a trade-off between a greater view from the nest and concealment. However, our analysis failed to identify other important habitat features at scales from 1–400 m from the nest. Our best-supported nest survival model showed a strong difference between our two main study areas, but this difference remains largely unexplained. Given the increased frequency, severity, and extent of wildfires predicted under climate change scenarios, our study highlights the importance of monitoring the persistence of boreal tundra patches and the Whimbrels breeding therein.

¹ Harwood, C.M., R.E. Gill, Jr. & A.N. Powell. 2016. Nesting ecology of Whimbrels in boreal Alaska. *Wader Study* 123(2): 99–113.

1.2 INTRODUCTION

Whimbrels *Numenius phaeopus* breed throughout the Holarctic, mostly in treeless, open habitats (Cramp & Simmons 1983). The North American subspecies *N. p. hudsonicus* (AOU 1998) nests in two disjunct regions, one confined mostly to Alaska and W Canada (i.e., the proposed *N. p. rufiventris*; Engelmoer & Roselaar 1998), and the other around Hudson Bay, Canada (Skeel & Mallory 1996). In northern and western Alaska, Whimbrels are considered widespread, discontinuous breeders beyond the treeline (Gotthardt *et al.* 2013). Within interior Alaska and NW Canada, however, Whimbrels appear to breed primarily in tundra-like patches, either in contiguous stretches (e.g., subalpine) or interspersed among boreal forests (Sinclair *et al.* 2003, Gibson 2011, Gotthardt *et al.* 2013). This area is characterized by a boreal forest-tundra ecotone comprising a vast mosaic of postfire communities, including lichen-shrub tundra and lichen-spruce woodlands (Payette *et al.* 2001). Yet despite the limited extent of tundra here (Jorgenson & Meidinger 2015) compared to sites in W and N Alaska, 50% (perhaps 20,000) of the western population of North American Whimbrels are thought to breed within the boreal forest biome (Wells & Blancher 2011, Andres *et al.* 2012).

This biome is characterized by disturbance, with wildfires arguably the most important factor shaping habitats, both spatially (local) and temporally (annual to decadal; Kasischke *et al.* 2010). The boreal region, however, is increasingly threatened by disturbances related to a warming climate and these act on larger (landscape-level) and longer (decades to centuries) scales (Grosse *et al.* 2011). Advancing tree line (Lloyd 2005), wetland drying (Riordan *et al.* 2006, Roach 2011), peatland loss (Frolking *et al.* 2011) increased shrubification (Tape *et al.* 2006), and more

active fire regimes (Kasischke & Turetsky 2006, Kasischke *et al.* 2010) are all hypothesized broad-based, long-term disturbances to this region that could further impact boreal tundra-like habitats in which Whimbrels currently breed.

In light of these predicted changes to boreal forest habitats, we studied the nesting ecology of Whimbrels breeding in interior Alaska, a region characterized by a continental climate and having an active wildfire regime (Kasischke *et al.* 2006). Indeed, this is the most comprehensive study of Whimbrels breeding in Alaska, and the first extensive breeding study of any boreal wader species in interior Alaska. We wanted to identify factors that may limit the distribution and nesting success of Whimbrels in their patchily distributed breeding habitats within the boreal forest biome. Our primary objective was to describe the nesting ecology of Whimbrels in tundra patches within the boreal forest, including metrics of phenology (arrival through hatch), nest density, and nest success. We also assessed habitat features at multiple spatial scales to determine their importance in the selection of nest sites (Jones & Robertson 2001, Bailey & Thompson 2007).

The Whimbrel is an aggressive attack-mobbing species that relies on early detection of predators (Skeel 1983, Skeel & Mallory 1996). We hypothesized that boreal-breeding Whimbrels would nest synchronously and in clusters to enhance joint nest defense. Further, because the placement of nests for many open-nesting bird species (including waders; Götmark *et al.* 1995, van der Vliet *et al.* 2008, Gómez-Serrano & López-López 2014) may represent a trade-off between concealment (e.g., landform, complexity of vegetative cover) and providing the incubating bird a clear view of its surroundings, we hypothesized that Whimbrels would select nest sites that were

elevated for view, yet still inconspicuous. We predicted that nesting earlier, nearer to conspecifics, and with fewer large obstacles (i.e., medium and tall shrubs, trees; Ballantyne & Nol 2011) to limit view from the nest, would increase Whimbrels' nest survival. Finally, we measured habitat preferences to predict how Whimbrels might respond to more woody environments projected under future climates (Lloyd 2005, Tape *et al.* 2006).

1.3 METHODS

1.3.1 Study area

We studied the nesting biology of Whimbrels from May to July during 2008–2012 and 2014 near the Kanuti River in Kanuti National Wildlife Refuge (NWR; 66.18°N, 151.74°W), approximately 235 km NW of Fairbanks, Alaska (Fig. 1.1). This lowland (165–180 m elevation) area features a diverse mosaic of boreal floodplain habitats including lakes and ponds, black spruce *Picea mariana* woodland, riparian mixed (e.g., *P. glauca*, *Betula papyrifera*, *Salix* spp.) forest, ericaceous shrub-*Sphagnum* bogs, tussock (*Eriophorum vaginatum*) tundra, mixed low/dwarf shrub (e.g., *Vaccinium* spp., *Ledum* spp., *B. nana*) and lichen (e.g., *Cladonia* spp., *Cladina* spp., *Flavocetraria* spp.) scrub meadow, and varyingly aged wildfire burns (i.e., most recently in 1977, 1991, and 2005).

During 2008–2010 we visited only the Kanuti Lake and Lake Taiholman study areas, with nest searching beginning in 2009 (Fig. 1.1). During 2011–2012 we expanded our search area to investigate tundra patches that were >0.5 km² and within a 20-km range along the Kanuti River (boatable) and ≤6 km from the river (walkable). We used ground and aerial reconnaissance, as

well as SPOT and LANDSAT imagery, to identify and locate patches. Given extensive avifaunal reconnaissance of all habitats within the greater study area during 2008–2010, we were confident that these identified patches comprised all potential breeding habitats for local Whimbrels. We intensively and repeatedly surveyed all such areas for Whimbrels in 2011 and 2012, ceasing visits once a patch was deemed unoccupied or territorial birds had not bred and had since departed. During 2014, our work was limited to the Kanuti Lake, Lake Taiholman, and Everglades study areas.

In all years, we arrived at Kanuti Lake no later than 1 May, a date prior to the first arrival of Whimbrels. Visits to Lake Taiholman, the Everglades, and the unnamed patches were constrained by logistics (e.g., ice-out of river) and did not occur until after the arrival of Whimbrels to those areas; consequences included potentially more conservative assessments of arrival and nest initiation, and less frequent nest checking, especially near hatch. In most years fieldwork extended into mid-July and spanned the entire nesting period, although biologists generally departed before the departure of juveniles and any attending adults.

1.3.2 Nest searching and monitoring

We surveyed the Kanuti Lake study area nearly daily on foot to document the arrival of Whimbrels and the subsequent occupancy of nesting territories. We visited Lake Taiholman and Everglades as soon as boat access permitted. Beginning about seven days after Whimbrel arrival and for \geq three weeks thereafter, we intensively searched nesting areas by walking the area and either flushing birds off nests or looking for courtship and nest defense activity. We recorded nest locations with a GPS, marked the nest with bare tree/shrub limbs 3 and 10 m north of the

nest to minimize visual cues to predators, and noted the number of eggs. We floated eggs of complete clutches (four eggs) to assess stage of incubation (after Liebezeit *et al.* 2007, Brown *et al.* 2014). Incubation was assumed to begin when the third egg was laid (CMH pers. obs., Skeel & Mallory 1996; and as observed in other *Numenius*; Marks *et al.* 2002, Hartman & Oring 2006) and to be 24 d long (Skeel & Mallory 1996). On average we checked nests every five days and followed protocols from Brown *et al.* (2014) for monitoring and assessing status and fates of nests.

1.3.3 Nesting habitat surveys

In 2011 and 2012 we characterized nesting habitat features at four spatial scales: landscape (up to 400 m), territory (10–50 m), nest area (1–10 m), and nest bowl (≤ 1 m). We duplicated all measurements at a paired non-nest point (‘random’ hereafter) located at a random bearing and distance (up to 50 m) from the nest, and avoided locating these points in unlikely Whimbrel nesting habitats (e.g., forest, tall shrub, water). The 50-m maximum distance for locating random points was to ensure that points were within a pair’s territory, based on observations of relatively close inter-nest distances from 2009–2010 (median = 105 m, range 76–131 m, $n = 5$). We deployed a 16-cm-diameter plastic disk to represent the ‘nest’ location when conducting measurements at random points. Sixteen cm closely approximated the size of local nest bowls. To minimize disturbance to incubating birds, we measured all habitat variables within one week post-hatch (or estimated hatch date for failed nests). To minimize temporal bias, we measured habitat features of a given year’s nests within a two-week span.

In 2011 we relocated nests found in 2009 and 2010. At these nests we collected the same habitat data as collected for the 2011 and 2012 nests to use in our nest survival analysis, but did not collect data for paired random points. We recognized that only the most persistent habitat features, such as the presence of a tree or taller shrubs, would likely be appropriate for inclusion in between-year comparisons one to two years after actual use. Thus, we avoided inclusion of more ephemeral features like water, or more dynamic features like plants that might exhibit sufficient annual growth to change cover or height categories.

The habitat variables assessed at the four spatial scales were:

Landscape (≤ 400 m). We measured the distance (m) to the nearest water (including small bogs and fens), and to dwarf (<20 cm tall), low (20–50 cm), medium (50–150 cm), and tall (>150 cm) shrubs and trees. At sites where shrubs were too distant to detect with a rangefinder, we substituted the maximum distance recorded among any nests/random; this allowed us to include all nests in the logistic regression nest-site selection analysis. Similarly, for sites where the distance to the nearest tree exceeded 400 m, we substituted a minimal value of 400 m.

Territory (10–50 m). We counted the number of trees, as well as the combined number of medium and tall shrubs, within 30 m of the nest/random for comparison with other studies. We also classified the major (>50%) and minor (<50%) habitat types by percentage within a 50-m radius according to the Alaska Vegetation Classification (Level IV; Viereck *et al.* 1992).

Nest area (1–10m). We quantitatively assessed microrelief, or roughness (Rodrigues 1994), within 10 m of the nest/random by stringing a level line over the nest/random in both east-west and north-south orientations. At 1-m intervals along each line (40 points in total), we measured the vertical distance (0.5-cm precision) to the surface or vegetative contact below or above the string with a 2-m folding rule. We assessed three features along the four 10-m radii: (1) surface roughness, defined as the standard deviation of the differences in heights between adjacent points ('AdjHt'); (2) height of the nest/random site relative to the mean height of the points ('RelCup'); and (3) percent covers based on surface type (e.g., plant form, water) at the 40 sample points ('Cover'). In addition, we summed the combined number of medium (50–150 cm) and tall (>150 cm) shrubs within 10 m of the nest/random ('Shrub'). To assess visibility of the nest we estimated the percentage (to nearest 5%) of a 16-cm plastic disk, placed at the nest/random, that was visible when observed at a height of 1 m and a distance of 3 m from each cardinal and intercardinal direction (see vegetation density estimation in Ballantyne & Nol 2011). Finally, we measured the absolute relief of the area, defined as the difference between the highest and lowest surface heights.

Nest bowl (0–1 m). We recorded if nests and random points were located on top of a hummock ('Hummock'). We calculated nest concealment ('Conceal') by adopting Skeel's (1983) assessment of 'nest protection' (percentage of times the nest cup/random had an adjacent mound [including tussock] or shrub >8 cm above nest cup/random in the four cardinal and four intercardinal directions). We photographed a 1-m² quadrat centered on the nest/random to estimate the non-overlapping percent cover of seven categories of cover: shrub, graminoid, forb, moss, lichen, dead organic matter, and water. Where needed, we photorectified images to remove any image distortion.

All photos were then analyzed with the software ‘SamplePoint’ (Booth *et al.* 2006), which features an automated, pixel-based point-intercept sampling procedure and summary calculation of percentages. We used a systematic sampling of 100 point-intercepts for each image. To assess cover complexity, we calculated the standard deviation in percent cover among the observed cover types for each nest/random (‘Cover’). Finally, we assessed roughness at this scale by sampling points at 10-cm intervals out to 1 m in each cardinal direction. We defined roughness (‘Rough’) here as the standard deviation of the differences in heights of the 40 points relative to the nest cup/random point heights; positive and negative values reflected heights above and below the nest/random, respectively.

1.3.4 Analyses

Breeding phenology. We used calculated initiation (i.e., laying of first egg) dates based on observed clutch completion dates (assuming 1 egg per day) where nests were found during laying, backdating from observed hatch dates using a 26-d exposure period where possible, or by using float angle data (Liebezeit *et al.* 2007) for nests that did not hatch or that were not revisited to determine fate (e.g., all nests in 2014). We used standard deviations to characterize heterogeneity or synchrony in dates (Nol *et al.* 1997, Smith *et al.* 2010).

Nest distribution. To assess the distribution of nests, we created study area polygons in ArcMap (ver. 10.1; Environmental Systems Research Institute, Redlands, CA) based on our GPS search track histories and ecotones indicated in our SPOT imagery basemaps, allowing us to estimate nest densities per areas searched. We followed recommendations in Fortin & Dale (2005) and used multiple tools to test whether Whimbrel nests were clustered or dispersed. When sample

sizes allowed, we used the ‘Multi-distance Spatial Cluster Analysis (Ripley’s K)’ and ‘Average Nearest Neighbor’ (ANN) tools in ArcMap’s ‘Spatial Analyst’ extension. Ripley’s K assesses if the average number of neighboring nests for a particular distance band is higher than the average concentration of nests throughout the study area; if so, the nests are considered clustered at that distance. ANN compares observed mean distance among nests to the expected mean distance (i.e., random distribution of nests).

Nest-site selection. We used an information-theoretic approach (Burnham & Anderson 2002) and logistic regression to evaluate support for specific habitat features in predicting nest location at the landscape, nest-area, and nest-bowl scales. We omitted a similar analysis at the territory scale because of redundancy in the variables measured. We ran correlation analyses on all two-way combinations of predictor variables and detected no problematic collinearity (all $r < 0.5$ and all $P > 0.05$). We selected variables for further analyses that (1) explicitly addressed our hypotheses, (2) allowed for comparison with other Whimbrel habitat selection studies, or (3) assessed habitat features previously undescribed or untested. This resulted in candidate sets of 16 models with 0–4 predictors for each spatial scale. We centered all covariates to improve interpretation of the relative strength of parameter estimates (Grueber *et al.* 2011) using a standard Z-transformation. Because the data set was small and we did not want to over-parameterize the models, we did not fit interaction models and we pooled results across years. We used the Hosmer-Lemeshow test statistic to confirm goodness-of-fit. We calculated AIC_C (Akaike’s Information Criterion, corrected for small sample size) weights for each supported model (i.e., those without uninformative parameters; Arnold 2010) in the candidate set. We summed the model weights ($\sum w_i$) for each variable using the individual weights of those models containing the respective variable.

When model-selection uncertainty was high, we model-averaged parameters to generate estimates, their 95% confidence intervals, and relative importance values. We considered model-averaged parameter estimates with 95% confidence intervals that did not overlap zero to be biologically meaningful, and we assessed effect size on a probability scale. Analyses were conducted using Program R.3.1.1 (R Development Core Team 2014) and packages MuMIn (Bartón 2014) and Resource Selection (Lele *et al.* 2014).

Nest survival. We used a similar information-theoretic approach to evaluate the relative support for potential factors influencing daily nest survival rate (DSR). We used Program MARK (White & Burnham 1999) to build a set of competing models following Rotella (2015). We first standardized the dates among all years such that the numbering started with the first nest found and ended with the last nest checked across all years (19 May–25 June; 38 d). We censored the only three nests (two in 2009, one in 2010) we located at Lake Taiholman because of the small sample size at that site. We first created models where DSR varied by ‘Year,’ ‘Site’ (Kanuti Lake vs. Everglades), and their interaction. We then considered 4 time- or stage-related models: (1) constant DSR through time (‘Constant’), (2) DSR varying across the nesting season (i.e., linear trend on the logit scale; ‘Season’), (3) DSR varying with nest age (‘NestAge’), and (4) DSR varying by nest age at the time of finding (‘FoundAge’). In 2009, we lacked information for six nests for assessing age so we assigned them the mean initiation date for that year to estimate relative nest age and age when found, and retained them in the models; we felt that was reasonable given the synchrony we observed that year. We built one model where DSR varied by inter-nest distance to explore the possible influence of intraspecific neighbors (‘InterDist’). Finally, we created two models with covariates for the number of medium and tall shrubs within 30 m

(‘Shrub’) and the presence of trees within 30 m of the nest (‘Tree’) to evaluate possible influence of greater woody growth on DSR (e.g., Ballantyne & Nol 2011). To estimate nest survival and its 95% confidence interval (CI), we used the estimates for DSR and lower/upper CI bounds each multiplied over the length of the exposure period (i.e., 26 d for this study).

Unless otherwise noted, means are presented \pm SD.

1.4 RESULTS

1.4.1 Breeding phenology

Mean first detection of Whimbrels among all years occurred on 6 May (Table 1.1). The first nest(s) were initiated 11.2 d (range: 8–14 d) after the first Whimbrels were detected. Mean nest initiation varied among years by less than one week, but there were up to 17 d between the earliest and latest recorded nests across years (Table 1.1). Nine nests that were found during laying were subsequently observed hatching, with mean and modal nest exposure lengths of 26.7 d and 26.0 d, respectively. Based on the modal exposure length and observed incubation patterns from nests with < four eggs, we inferred a 24-d incubation period beginning with the laying of the third egg. Hatch generally occurred in the third week of June (17 June \pm 3.3 d, n = 70 nests; Table 1.1).

1.4.2 Nesting distribution and densities

During 2010–2012 we visited all or most of nine tundra areas (mean size: $2.64 \pm 2.35 \text{ km}^2$) to identify potential habitat for Whimbrel breeding (Fig. 1.1). We observed no Whimbrels in the three smallest patches ($0.54\text{--}0.87 \text{ km}^2$), which were also areas with the largest perimeter-to-area ratios ($5.8\text{--}10.2$). We observed at least one displaying male in the six largest patches ($1.49\text{--}7.20 \text{ km}^2$), including confirmed nesting at Kanuti Lake (2008–2012, 2014), Lake Taiholman (2008–2010), and Everglades (2011–2012, 2014; Fig. 1.2). The areas with confirmed nesting had three of the four lowest perimeter-to-area ratios ($2.0\text{--}4.4$).

Nesting density at Kanuti Lake declined by at least 65% between 2009 and 2011 (from 2.67 to 0.94 nests/km^2) before rebounding in 2012 (1.57 nests/km^2). At Lake Taiholman at least two pairs nested in 2008 and 2009, and one pair nested in 2010, but no birds were detected there in 2011–2014, despite repeated annual visits. The Everglades population densities ($1.53\text{--}1.67 \text{ nests/km}^2$) were similar to that of Kanuti Lake in 2012. Overall, mean distance between nests was 318 m (range $64\text{--}926 \text{ m}$, $n = 46$ nests, 2009–2012) and 372 m (range $160\text{--}694 \text{ m}$, $n = 23$ nests, 2011–2012) for Kanuti Lake and Everglades, respectively.

Because our sample sizes fell short of those recommended (i.e., <30) for the ANN and ‘Ripley’s K’ cluster analyses, we restricted final interpretation to each area’s most populous and densest nesting year. Clustered nesting was suggested for Kanuti Lake in 2009 (ANN nearest neighbor ratio = 0.72 , $Z\text{-score} = -2.179$, $P = 0.029$; Ripley’s K ‘clustered’ distance beginning at $\sim 300 \text{ m}$). Dispersed nesting, however, was weakly suggested at the Everglades in 2012 (nearest neighbor ratio = 0.99 , $Z\text{-score} = -0.040$, $P = 0.968$; Ripley’s K ‘clustered’ distance = $\geq 850 \text{ m}$).

1.4.3 Breeding habitat characterization

We characterized habitat features at 17 and 22 confirmed nesting territories in 2011 and 2012, respectively. ‘Mixed shrub-sedge tussock bog’ (Vioreck *et al.* 1992; level IIC2b) was the primary habitat characterizing Whimbrel territories (≤ 50 m from the nest) in the study area, composing on average 69% of each territory. Territories included six other habitat classifications, including three more of the ‘open low scrub’ type (level IIC2, but non-tussock) and three ‘wet graminoid herbaceous’ types (level IIIA3), accounting for 14% and 17% of the territories, respectively. Trees and tall (>150 cm tall) shrubs tended to be both distant and scarce; 41% of nests had no trees and 36% had no tall shrubs within 100 m. Nests were typically near water (Table 1.2). Non-overlapping percent cover within 1 m and 10 m of nests was similar for the seven functional ‘vegetative’ types, despite the difference in scales, with shrubs and graminoids as most abundant in each (Table 1.2).

1.4.4 Nest-site selection

Landscape (0–400 m) and nest area (1–10m) scales. At the landscape scale, none of the models with factors representing distances from the nest/random to nearest woody vegetation (i.e., low, medium, and tall shrubs; tree) were supported (Table 1.3). At the nest area scale, the model with the lowest AIC_C included only the surface roughness variable ‘AdjHt’ (Table 1.4). This was the only model ranked higher, albeit only slightly ($\Delta AIC_C = 0.79$; coefficient estimate \pm SE: 0.23 ± 0.27), than the null model, and it passed the Hosmer-Lemeshow goodness-of-fit test ($\chi^2 = 8.6$, $df = 8$, $P = 0.38$). The competing models at these two scales of habitat selection generally showed little separation.

Nest bowl (0–1 m) scale. The best-supported AIC_c model included the variables Hummock, Conceal, and Cover and accounted for 35% of the AIC_c weight (Table 1.5). The similarly parameterized full model, but also including the variable Rough, differed only slightly ($\Delta AIC_c = 0.09$) from the former; these two models accounted for 68% of the cumulative AIC_c weight. However, unlike the top-ranked model ($\chi^2 = 10.7$, $df = 8$, $P = 0.219$), the full model did not pass the Hosmer-Lemeshow goodness-of-fit test ($\chi^2 = 15.9$, $df = 8$, $P = 0.044$). Another seven models were within 10 AIC_c units of the top-ranked model and captured 100% of the AIC_c weights; we model-averaged over these nine models to test the probability of nest occurrence. The location of a nest on a hummock was the most important predictor of nest selection, with percent of nest concealed having 93% relative importance to Hummock. The probability of a nest occurring on a hummock was 49% higher than it not being on a hummock. Further, the probability of nest occurrence increased by 0.16 for each additional direction (of eight possible) providing concealment at the nest rim. The 95% confidence intervals for the estimates of the Cover and Rough coefficients overlapped zero, suggesting they were not biologically meaningful predictors of nest bowl location.

1.4.5 Nest survival

We modeled factors affecting nest survival using data from 67 nests, including 16, 13, 6, and 10 for Kanuti Lake 2009–2012, and 10 and 12 for Everglades 2011–2012, respectively. The model receiving the greatest support ($w_i = 0.79$) among those in the candidate set included the single factor Site (Table 1.6). This model was 5.6 times more likely than the second-ranked interaction

model Site*Year, which was based on very small sample sizes per site per year; other candidate models had little support. Using DSR estimates derived from the top-ranked model, overall nest survival during the 26-d exposure period was estimated to be 41% (95% CI: 26–55%) at Kanuti Lake and 92% (95% CI: 55–99%) at the Everglades across the years monitored at each site.

1.5 DISCUSSION

1.5.1 Distribution and timing of nesting

The discreteness and relatively small area of tundra patches in our study area appeared to spatially limit Whimbrels' breeding. In other ecosystems, the occurrence and abundance of birds within habitat patches is a function of multiple factors, including patch-scale variables like size, habitat condition, shape, and perimeter, and landscape-scale variables like configuration of patches and the habitat matrix surrounding patches (Mazerolle & Villard 1999, With & King 2001, Fleishman *et al.* 2002, Blevins & With 2011). The absence of Whimbrels occupying the smallest patches of tundra in our study area suggests a possible threshold. Patches where Whimbrels displayed but did not nest may suggest inferior habitat conditions, including: (1) high perimeter-to-area ratios deemed by prospective breeding females as insufficient distance between a nest and possible predators in the ecotone (Andren & Angelstam 1988); (2) increasingly higher and denser shrub structure within the display area; or (3) extensive and severe, recently (2005) burned areas.

The nature of the boreal tundra patches in our study area is markedly different from more continuous tundra areas beyond the treeline (McCaffery 1996). Patches in our study area are

similar to other Whimbrel breeding areas that are bounded by natural (e.g., rivers, coastlines) or man-made ecotones (e.g., clearcuts, roads, airports; Pulliainen & Saari 1993, Ballantyne 2009, Pirie *et al.* 2009, Katrínardóttir 2012, Ballantyne & Nol 2015). However, these other sites exhibit multiple breeding habitat types or patches with varying functional connectivity between habitats, conditions not encountered in our study area (Fig. 1.3). Further, we cannot ignore the temporal limitations of this study (six years) in characterizing the breeding occupancy at the patch level. For example, at least one pair nested at the Lake Taiholman study area historically (1993–1995; Kanuti NWR unpubl. data) and in 2008–2010, but not thereafter.

The breeding phenology of Whimbrels in our study area showed pronounced annual consistency, with arrival, mean nest initiation and mean date of hatch varying by only 5 d across years. Further, mean hatch occurred only about six weeks after the first Whimbrels arrived, suggesting a compressed schedule; no nests hatched (or were scheduled to hatch) after 26 June. Grant (1989) documented annual initiation ranging over periods of 26–31 d for Whimbrels nesting in temperate Shetland, more than twice the longest initiation period that we observed. In 2010 and 2012, in which initiation in our study area occurred over about two weeks, the latest nests ($n = 4$) all failed, including three that were abandoned. This suggests that late nesting at this site is not generally successful (e.g., Smith *et al.* 2010), perhaps because this northern latitude and boreal climate impose a shorter window for successful breeding.

Given the spatial and temporal constraints imposed on Whimbrels breeding in our study area, we had hypothesized that predators might more efficiently target nesting Whimbrels here; in turn, these Whimbrels might nest in ways that facilitate cooperative nest and chick defense (i.e.,

clustered and synchronous nesting). Support for this premise was equivocal. We documented fairly synchronous nesting in 2009 and 2011, but less so in 2010 and 2012; however, we recognize that the compressed breeding schedule here necessarily increases synchrony more so than at sites with longer seasons. Clustered nesting was suggested for Kanuti Lake in 2009, but not for the Everglades. Despite these inconsistent results, nests may still be close enough for neighboring pairs to jointly mob effectively.

1.5.2 Nesting habitat and nest-site selection

Whimbrels nesting in our study area encounter a diverse suite of avian and terrestrial predators that vary in hunting behavior. This diversity of predators could demand potentially conflicting nest protection strategies, such as timely predator detection and nest crypsis. Our hypothesis that Whimbrels here would optimize a trade-off between nest concealment and view to limit predation was partly supported: nesting on a hummock (thus providing greater view) and greater lateral nest concealment were both shown to be important factors in nest-site selection at the smallest scale. Hummock use has been widely documented in Whimbrels (Ballantyne & Nol 2011). Our result provides further support that hummocks may be important for early detection of aerial predators. However, Ballantyne & Nol (2011) proposed an alternate hypothesis that hummocky sites melt out earlier, as is true in our study area, and this is advantageous to early nesting species such as Whimbrels. Unlike Skeel (1983), who attributed lateral protrusions of vegetation at nests to protection from prevailing winds, we believe this attribute to be more locally important as camouflage. Our finding of marginal support for nesting areas having greater surface roughness may be further evidence for the importance of habitat complexity (e.g., pattern disruption, increased shadow) in nest concealment, as also suggested by Skeel (1983).

Several other measures of complexity, however, were not shown to be important predictors of habitat use in our study.

We found little support for predictors of nest-site selection at larger spatial scales. This could be explained in several ways. For example, the 50-m ‘territorial’ radius may have been too small to reveal differences between nest and random point locations, given the relative homogeneity of the habitat. Other studies (Pirie 2008, Ballantyne & Nol 2011) used larger distances (250 and 150 m, respectively) in their nest-site selection investigations. Another factor could have been the timing of our habitat measurements. While collecting habitat measurements after nests have hatched is a common practice, this delay risks missing early habitat distinctions evident to Whimbrels during nest-prospecting, such as patterns of snow melt and pre-leaf-out vegetative cover.

Alternatively, some of our seemingly equivocal habitat selection results may actually be representative for Whimbrels breeding within tundra patches in boreal forest. These birds may simply be generalists at certain scales when selecting a nest site within a suitable patch of habitat. The species has a demonstrated flexibility in nesting habitat selection at the landscape or patch scale throughout other parts of its range. Whimbrels outside of Alaska have been documented nesting in multiple habitat types including hummock-bog, sedge meadow, heathland tundra, riverplain, and even mountain birch forest (Skeel 1983, Pulliainen & Saari 1993, Katrínardóttir *et al.* 2015). We observed Whimbrels using sites with varying levels of surface roughness, cover heterogeneity, and woody vegetation near the nest, but these may represent minor variations within the nest-site selection repertoire of this widely distributed species.

1.5.3 Nest survival

Ultimately we found little support for our hypotheses that nesting earlier, nearer to conspecifics, and with fewer large obstacles near the nest were important factors for nest survival. However, we did find a very strong site effect between our two main study areas; DSR was consistently higher at the Everglades than at Kanuti Lake. Other studies have documented that Whimbrels nesting in different habitat types may experience different levels of nest success (Skeel 1983, Pulliainen & Saari 1993, Katrínardóttir *et al.* 2015). Although we characterized Whimbrel territories similarly at the two sites, we did note coarse differences not necessarily captured by our assessments; for example, we noted a dominance of string bogs at Everglades, but less so at Kanuti Lake. Further, the most recent wildfires at Everglades and Kanuti Lake occurred in 1977 and 2005, respectively. Burn perimeters and unburned inclusions are evident at both sites, with Whimbrels nesting among them; however, vegetation recovery at Everglades was more advanced (e.g., no mineral soil visible, less burned duff, more lichen). Whether the likely wetter and less recently burned habitats of the Everglades impart advantages in nest survival is unknown.

Contrary to our expectations, the presence of nearby trees and large shrubs did not influence nest-site selection or impair nest survival. Whimbrels breeding in our study area appeared to tolerate, and to some extent even exploit (e.g., as sentry perches; Fig. 1.3), scattered black spruce in the tundra. Indeed, the three major breeding concentrations ('east' and 'west' Kanuti Lake, Everglades; Fig 1.2) partly surround conspicuous, isolated black spruce groves (*ca.* 0.01–0.03 km²) within the tundra patches, with nests as close as 10 m to the groves. Scattered medium and tall shrubs also were not strongly avoided. While we do not know what threshold of tree and shrub cover will be tolerated, we have observed Whimbrel occupying much shrubbier sites

elsewhere in the species' range (e.g., Donnelly Training Area, Alaska; CMH unpubl. data). However, for Whimbrels attempting to breed in small tundra patches like those at Kanuti NWR, increased woody vegetation within the patch and encroachment of trees and shrubs inward from the edge could jeopardize the persistence of these patches as open habitats. The increases in shrub and tree cover recently documented at Churchill, Manitoba, Canada, have likely contributed to a decline of Whimbrels there (Ballantyne & Nol 2015), and similar habitat changes have also been predicted for Alaska under a warming climate scenario (Lloyd 2005, Tape *et al.* 2006).

1.5.4 Boreal-nesting Whimbrels and wildfire

The active fire history that regularly and dynamically affects our area (e.g., 27% of Kanuti NWR burned in 2004–2005; USFWS 2008) has not been documented in other areas where Whimbrels have been studied. Although wildfires are frequent within the greater Hudson Bay Lowlands (Brook 2006), Whimbrels breeding near Churchill appear to use areas just outside this fire regime (Fig. 2.2 in Ballantyne 2009), perhaps a result of the proximity of these areas to the maritime influence of Hudson Bay. In general, we lack a perspective on how Whimbrels respond to major stochastic events that have impacted their landscapes (but see Katrínardóttir *et al.* 2015). During our study, we observed annual fluctuations in numbers and distribution, but we do not know how Whimbrels in the Everglades and Kanuti Lake areas responded immediately after wildfires in 1977 and 2005, respectively.

Within the already dynamic landscape of boreal Alaska, we may be witnessing additional effects on habitats from the projected increase in landscape flammability across the boreal forest during

the coming century (Rupp & Springsteen 2009, Johnstone *et al.* 2011). The possible amplification of the area's historical wildfire regime by a warming climate may pose a major threat to not only forested habitats (e.g., conversion of spruce to deciduous), but could result in the loss or modification (e.g., increased shrubs) of boreal tundra patches suitable for Whimbrel breeding. Studies of predicted changes in the boreal biome have focused on forests proper, and studies of tundra fires have targeted areas beyond the treeline (Higuera *et al.* 2011), not tundra patches within the boreal. Studies like ours can serve as baselines for monitoring these scattered tundra patches, and the persistence of Whimbrels therein. Further, replication of our study in other areas offers an approach to improve inference from local studies like ours ('metareplication'; Johnson 2002). Our research clearly shows the benefit of conducting regular surveys of historical Whimbrel breeding areas accessible within the boreal forest to document the local persistence of the species and to characterize its habitat. We especially urge a timely survey of a recently burned breeding areas to assess any changes to habitats and responses by the local Whimbrel population to wildfire effects. In time we can begin to better assess the vulnerability of Whimbrels and their habitats in a rapidly changing boreal biome.

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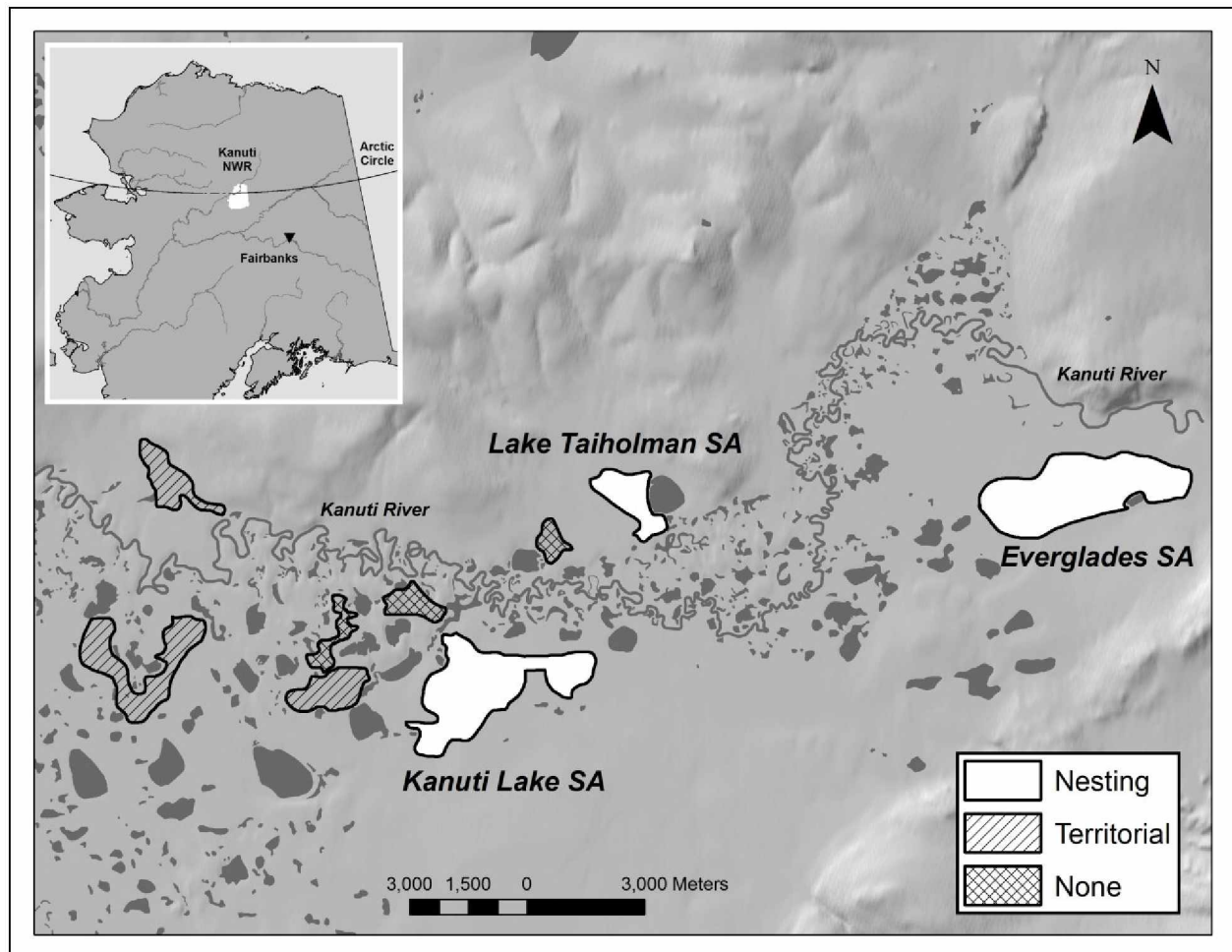


Fig. 1.1. Location of the study areas comprising nine tundra patches searched for Whimbrels within the Kanuti National Wildlife Refuge, Alaska, during 2008–2014. The legend depicts the assessment of occupancy or breeding status documented for each patch, with the major study areas indicated (SA).

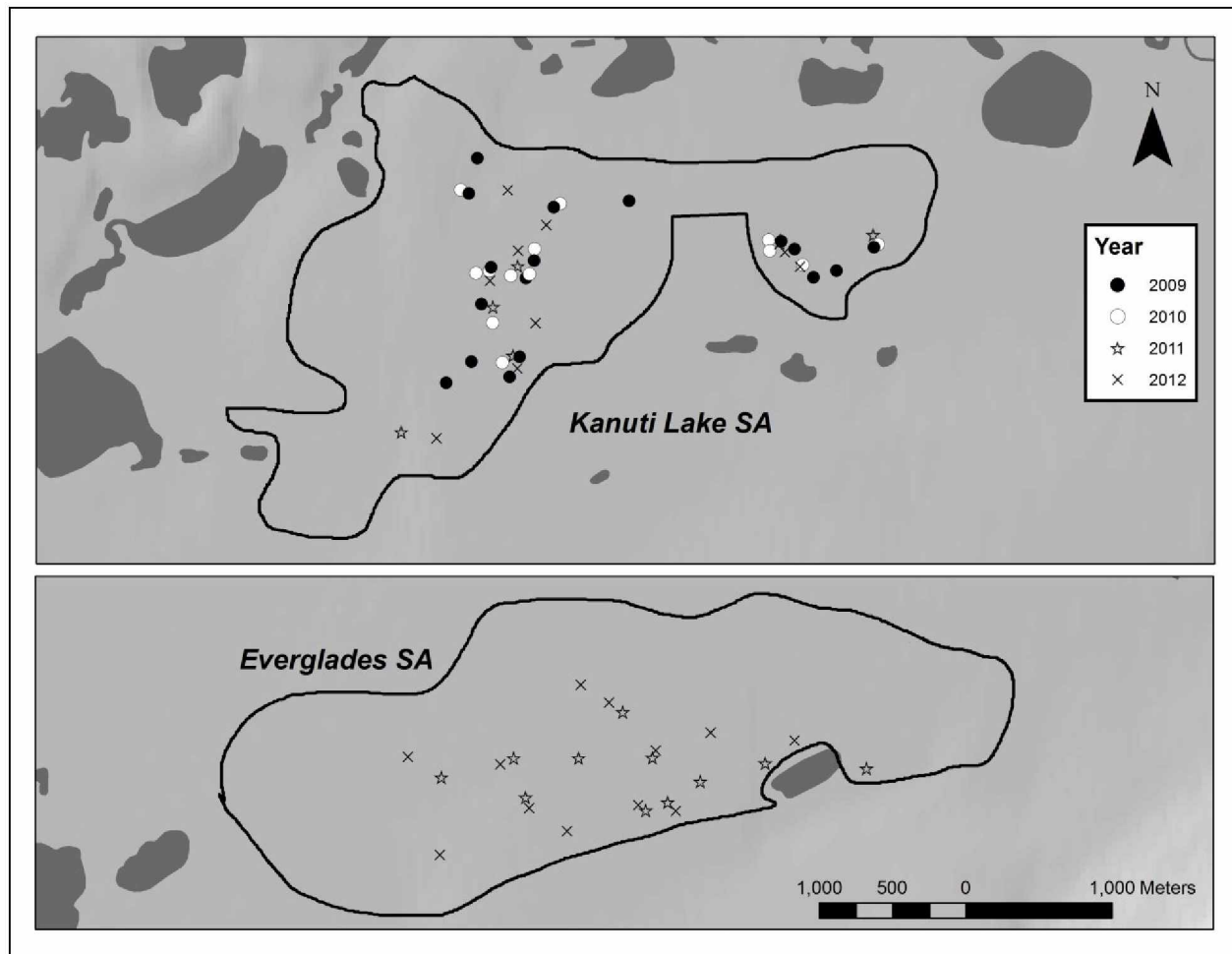


Fig. 1.2. Distribution of Whimbrel nests at Kanuti Lake and Everglades study areas (SA), Kanuti National Wildlife Refuge, Alaska, 2009–2012. The polygons represent the areas that were searched annually for Whimbrels, roughly representing discrete tundra patches. Vegetative ecotones surrounding these tundra patches are not depicted in the figure. Both maps are at the same scale. Symbols for each year's nests apply to both SAs shown.



Fig. 1.3. Representative photo of tundra patches in our study area (the Kanuti Lake patch) with a Whimbrel perched on the tallest black spruce in the foreground. Here patches are typically surrounded by a combination of waterbodies, hills, or wooded areas like the black spruce woodland in the distance, with no tundra connectivity between patches to allow family movements.

Table 1.1. Breeding phenology of Whimbrels nesting on the Kanuti River study area, Alaska, 2008–2014.

Year	# Nests found	First detection	Mean initiation date¹	Mean hatch date¹
2008	NA ²	6 May	NA	NA
2009	19	4 May	20 May \pm 1 18–21 May (11)	15 June \pm 1 13–16 June (11)
2010	14	8 May	24 May \pm 4 17–31 May (14)	19 June \pm 4 12–26 June (14)
2011	17	6 May	22 May \pm 1 20–24 May (17)	17 June \pm 1 15–19 June (17)
2012	22	7 May	23 May \pm 4 18–31 May (22)	18 June \pm 4 13–26 June (22)
2014	8	6 May	20 May \pm 3 14–23 May (6)	15 June \pm 3 9–18 June (6)

¹ mean \pm SD, range, and (*n*).

² NA = not available (Nests were not searched for, but broods were observed).

Table 1.2. Select habitat measurements (mean, SD, range) at four scales of distance from Whimbrel nests ($n = 39$) and from random points within the nest territory, Kanuti Lake and Everglades study areas, Alaska, 2011–2012.

Scale	Variable	Nest	Random
0–400 m	Distance to water (m)	2.3 ± 5.3 0.3–31.0	3.3 ± 2.9 0.0–10.9
	Distance to dwarf shrub (m)	0.0 ± 0.0 0.0–0.1	0.0 ± 0.0 0.0–0.1
	Distance to low shrub (m)	1.0 ± 0.7 0.0–3.0	1.1 ± 1.1 0.1–5.6
	Distance to medium shrub (m)	17.3 ± 21.9 1.4–109.0	14.1 ± 17.4 1.2–80.0
	Distance to tall shrub (m)	60.3 ± 56.6 5.9–208.0	49.9 ± 48.9 2.2–185.0
	Distance to tree (m)	130.4 ± 138.0 9.0–400.0	133.2 ± 137.9 10.5–400.0
10–50 m	# of medium & tall shrubs	18.6 ± 25.5 0–95	18.5 ± 26.2 0–125
	# of trees	0.6 ± 1.6 0–9	0.4 ± 1.1 0–6
1–10 m	Percent visible	54.2 ± 20.4 6.4–90.6	82.5 ± 17.5 31.9–100.0
	Absolute relief (m)	0.67 ± 0.45 0.03–2.1	0.69 ± 0.38 0.3–1.9
	# of medium & tall shrubs	3.6 ± 5.3 0–22	3.5 ± 5.6 0–25
	Percent graminoid	24.3 ± 14.9 5.0–65.0	21.1 ± 9.9 0.0–45.0
	Percent forb	2.6 ± 3.6 0.0–12.5	2.6 ± 3.8 0.0–20.0
	Percent lichen	14.5 ± 10.2 0.0–32.5	16.0 ± 10.8 0.0–40.0
	Percent moss	17.2 ± 9.8 0.0–40.0	16.4 ± 8.6 2.5–37.5
	Percent organic matter	3.5 ± 5.0 0.0–22.5	4.2 ± 5.7 0.0–22.5
	Percent shrub	35.1 ± 10.7 15.0–55.0	38.5 ± 9.5 25.0–57.5
	Percent water	2.8 ± 5.4 0.0–27.5	1.4 ± 3.4 0.0–15.0
	Concealment (%)	0.4 ± 0.2 0.0–0.9	0.3 ± 0.2 0.0–0.8
	SD of percent cover	14.2 ± 2.7 9.1–21.5	15.0 ± 3.2 8.9–24.2
0–1 m	Height diff.: nest vs. intercept (cm)	-2.5 ± 3.2 -9.8–6.0	-0.9 ± 4.4 -12.1–8.4
	Percent graminoid	24.5 ± 13.8 3.1–60.0	21.9 ± 13.8 0.0–64.9
	Percent forb	3.6 ± 4.5 0.0–18.1	3.5 ± 4.3 0.0–14.4
	Percent lichen	18.9 ± 12.1 0.0–44.3	18.8 ± 13.4 0.0–49.0
	Percent moss	16.0 ± 8.0 0.0–34.0	16.7 ± 9.4 1.0–39.0
	Percent organic matter	7.7 ± 5.2 0.0–28.9	7.7 ± 8.2 0.0–48.5
	Percent shrub	29.1 ± 10.1 7.5–58.5	31.5 ± 11.1 4.3–50.0
	Percent water	0.2 ± 1.0 0.0–6.2	0.0 ± 0.0 0.0–0.0

Table 1.3. Logistic regression model selection results used to predict Whimbrel nest-site selection (nest vs. random point within the territory) as a function of four habitat variables measured within a scale of 0–400 m from the nest or random point, Kanuti Lake and Everglades study areas, Kanuti National Wildlife Refuge, Alaska, 2011–2012. Models are ordered by Akaike’s Information Criterion, corrected for small sample size (AIC_c). K is the number of parameters, ΔAIC_c is the AIC difference from the top model, and -LL is the negative log-likelihood, a measure of deviance. The four variables considered were distances to nearest low shrub (Low), medium shrub (Medium), tall shrub (Tall), and tree (Tree). The 16 candidate models were ultimately averaged. No models received greater support than the null model so model weights were not calculated/shown.

Model	K	ΔAIC_c¹	-LL
Null	1	0.00	54.07
Low	2	1.63	53.83
Medium	2	1.66	53.84
Tall	2	1.98	54.00
Tree	2	2.10	54.06
Med + Low	3	3.10	53.48
Tree + Medium	3	3.61	53.74
Tall + Low	3	3.69	53.77
Tree + Low	3	3.80	53.83
Tall + Medium	3	3.81	53.83
Tree + Tall	3	4.07	53.96
Tree + Medium + Low	4	5.13	53.38
Tall + Medium + Low	4	5.33	53.48
Tree + Tall + Medium	4	5.74	53.69
Tree + Tall + Low	4	5.88	53.76
Tree + Tall + Medium + Low	5	7.39	53.37

¹ AIC_c value of the top model is 110.18.

Table 1.4. Logistic regression model selection results used to predict Whimbrel nest-site selection (nest vs. random point within the territory) as a function of four habitat variables measured at a scale of 0–10 m from the nest or random point, Kanuti Lake and Everglades study areas, Kanuti National Wildlife Refuge, Alaska, 2011–2012. Models are ordered by Akaike’s Information Criterion, corrected for small sample size (AIC_c). K is the number of parameters, ΔAIC_c is the AIC difference from the top model, and -LL is the negative log-likelihood, a measure of deviance. The four variables tested included measures of (1) surface roughness (AdjHt) and (2) relative height of nest to surrounding surfaces (RelCup), (3) cover heterogeneity (Cover), and (4) number of medium or tall shrubs (Shrub). The 16 candidate models were ultimately averaged. Only the model with ‘AdjHt’ variable received even marginal support over the null model; thus, model weights were not calculated/shown.

Model	K	ΔAIC_c¹	-LL
AdjHt	2	0.00	52.62
Null	1	0.79	54.07
RelCup + AdjHt	3	1.95	52.51
Shrub + AdjHt	3	2.16	52.62
Cover + AdjHt	3	2.16	52.62
RelCup	2	2.59	53.91
Cover	2	2.78	54.01
Shrub	2	2.89	54.06
Shrub + RelCup + AdjHt	4	4.17	52.51
RelCup + Cover + AdjHt	4	4.18	52.51
Shrub + Cover + AdjHt	4	4.38	52.62
RelCup + Cover	3	4.65	53.86
Shrub + RelCup	3	4.75	53.91
Shrub + Cover	3	4.94	54.01
Shrub + RelCup + Cover + AdjHt	5	6.45	52.51
Shrub + RelCup + Cover	4	6.87	53.86

¹ AIC_c value of the top model is 109.39.

Table 1.5. Logistic regression model selection results used to predict Whimbrel nest-site selection (nest vs. random point within the territory) as a function of four habitat variables measured at a scale of 0–1 m from the nest or random point, Kanuti Lake and Everglades study areas, Kanuti National Wildlife Refuge, Alaska, 2011–2012. Models are ordered by Akaike’s Information Criterion, corrected for small sample size (AIC_c). K is the number of parameters, ΔAIC_c is the AIC difference from the top model, w_i is AIC_c weight, and -LL is the negative log-likelihood, a measure of deviance. The four variables tested included (1) whether nest was on a hummock (Hummock), (2) nest concealment (Conceal), (3) cover heterogeneity (Cover), and (4) an alternate measure of roughness (Rough). The candidate models contributing to the cumulative AIC_c were ultimately averaged. Model weight for model named ‘Cover’ (ranked lower than Null) was not calculated.

Model	K	ΔAIC_c¹	w_i	-LL
Hummock + Conceal + Cover	4	0.00	0.35	38.10
Hummock + Conceal + Cover + Rough	5	0.09	0.33	37.00
Hummock + Conceal	3	1.68	0.15	40.06
Hummock + Conceal + Rough	4	2.65	0.09	39.42
Hummock	2	5.55	0.02	43.07
Hummock + Cover + Rough	4	5.89	0.02	41.05
Hummock + Rough	3	6.13	0.02	42.28
Hummock + Cover	3	6.22	0.02	42.32
Conceal + Cover + Rough	4	8.77	0.00	42.49
Conceal + Rough	3	13.11	0.00	45.77
Conceal + Cover	3	16.40	0.00	47.41
Cover + Rough	3	16.48	0.00	47.45
Rough	2	18.00	0.00	49.30
Conceal	2	18.40	0.00	49.50
Null	1	25.43	0.00	54.07
Cover	2	26.28	-	53.43

¹ AIC_c value of the top model is 84.75.

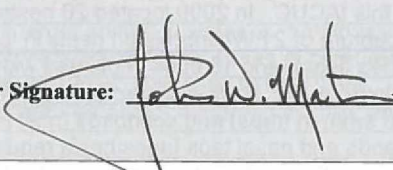
Table 1.6. Model selection results for analysis testing potential factors of daily survival rate (DSR) for Whimbrel nests at Kanuti Lake and Everglades study areas, Kanuti National Wildlife Refuge, Alaska, 2009–2012. Models are ordered by Akaike’s Information Criterion, corrected for small sample size (AIC_C). K is the number of parameters, ΔAIC_C is the AIC difference from the top model, w_i is AIC_C weight. The ten models tested DSR of nests (1) ‘Constant’ through season; and then varying (2) through ‘Season’, (3) by ‘Year’, (4) by study area (Site), (5) by Site*Year interaction, (6) by age of nest (NestAge), (7) by age of nest when found (AgeFound), (8) by nearest inter-nest distance (InterDist), (9) by number of nearby large shrubs (Shrub), and (10) by presence of nearby trees. Model weights were not calculated for unsupported models (i.e., ranked lower than the constant model).

Model	K	ΔAIC_C¹	w_i	Deviance
Site	2	0.00	0.79	162.01
Site*Year	6	3.44	0.14	157.37
Season	2	5.46	0.05	167.47
AgeFound	2	9.08	0.01	171.09
Constant	1	9.28	0.01	173.29
NestAge	2	9.60	-	171.60
Year	4	9.97	-	167.95
Tree	2	10.19	-	172.20
Shrub	2	10.98	-	172.99
InterDist	2	11.16	-	173.16

¹ AIC_C value of the top model is 166.02.

Appendix 1.A. IACUC authorization for Whimbrel studies on Kanuti NWR, 2010–2012.

Assurance of Animal Care Form

IACUC Use Only	
IACUC Number: <u>2010007</u>	USDA Classification: <u>C / D / E</u> (Circle One)
Date Received: _____	Initial Review Date: _____
IA Training Complete: <input checked="" type="checkbox"/> te: <input checked="" type="checkbox"/>	
IACUC recommendations: Approved: <input checked="" type="checkbox"/> Not Approved: <input type="checkbox"/>	
Date Revisions Received: _____	Initial Approval Date: _____
Renewal Month: _____	First Annual Renewal Date: _____
	Second Annual Renewal Date: _____
IACUC Chair Signature: 	Date: <u>21 MAY 2010</u>

Project Title:

Breeding Biology and Habitat Use of Whimbrels on Kanuti NWR

Name(s) of Funding Source(s): FWS Kanuti NWR base funding

Approximate Starting Date: 1 May 2010 Completion Date: 15 July 2012 Ongoing ☐

I. PERSONNEL

Principal Investigator: Christopher M. Harwood

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Mailing Address: Kanuti NWR, 101 12th Ave., Rm 262, Fairbanks, AK 99701

Due to the remote location of many USFWS field stations and the fact the PI may not be on site during the entire project, please designate an alternate local responsible individual and provide the contact name and phone number for use in case of emergency, after hours problems, or if the PI cannot be contacted for time sensitive decisions or concerns regarding the project. This person should be able to assume responsibility for decisions or actions necessary to ensure health and welfare in the event of unanticipated problems. If the responsible individual cannot be contacted, the FWS Region 7 IACUC will assume responsibility and take actions deemed necessary to ensure appropriate animal care.

Local (Field Station) Contact: Kanuti NWR Name: Mike Spindler__ Phone #: 388-0687 (c)

Personnel Qualifications:

Chapter 2. Occurrence of Whimbrels during the breeding season in interior Alaska.¹

2.1 ABSTRACT

Observations of Whimbrels *Numenius phaeopus* during the breeding season in Alaska's vast Interior are relatively few and patchily distributed, likely generally reflecting both the species' distribution and challenges in surveying them. I designed a Whimbrel-specific survey to better understand their distribution in interior Alaska, including developing an explanatory model to refine habitat and avifaunal associations of Whimbrels to help future development of predictive models of their distribution at a larger scale. I also wanted to identify possible conservation areas and sites for more targeted research and monitoring. First, I used existing literature and canvassed ornithologists to develop a GIS-based map of likely Whimbrel breeding habitat accessible from Alaska's road system. Three field crews used this map to conduct 279 point counts along 28 transects distributed among the Dalton, Denali, Elliot, Parks, Richardson, Steese, and Taylor Highways between 23 May–20 June 2013 and detected Whimbrels on 9 (32%) transects and 31 (11%) points. We added 3 new general locations for Whimbrels along the Elliot (2 sites) and Dalton Highways; however, no Whimbrels were detected along the Taylor (highly forested) and Steese Highways. We confirmed breeding in 2013 at Chandalar Shelf and Stampede Road, the latter recognized as a promising site for possible future intensive studies. Dwarf shrub meadow was the predominant habitat at points where Whimbrels were (56%) and were not (45%) detected. I used a binomial generalized linear mixed-effects model to evaluate the importance of specific habitat and avifaunal community features to the presence of Whimbrel

¹ Harwood, C.M. 2016. Occurrence of Whimbrels during the breeding season in interior Alaska. Prepared for submission in *Wader Study*.

at our count points; no feature was shown to be important. My results from interior Alaska further support the following general inferences about the breeding ecology of Whimbrels: they are patchily distributed, exhibit clustered nesting, and breed in a variety of open-country habitats.

2.2 INTRODUCTION

Studies of North American Whimbrels *Numenius phaeopus* during the breeding season remain limited, despite the species' official designation of conservation concern by multiple governmental and conservation entities in Canada (Donaldson *et al.* 2000) and the United States (Alaska Shorebird Group 2008, U.S. Shorebird Conservation Plan Partnership 2016). Effective conservation actions for any species depend on knowledge of basic life history parameters, in particular knowledge of breeding season distribution, but even this is largely unknown for nearctic-nesting Whimbrels and especially for Whimbrels breeding within Alaska's vast boreal Interior (Gibson 2011, Gotthardt *et al.* 2013). Discontinuous tundra-like habitats in the Interior (see Jorgenson and Meidinger 2015), the ostensibly patchy distribution of Whimbrels throughout their range (Cramp & Simmons 1983, Skeel & Mallory 1996, Harwood *et al.* 2016), and surveyors' difficulty in accessing portions of Alaska's vast Interior, have all contributed to this lack of knowledge.

The overall objective of my work was to characterize and identify factors that explained the occurrence of Whimbrels at my study sites, with the intent that this information could ultimately be incorporated into models predicting the occurrence of Whimbrels across larger spatial scales.

Towards this objective I retrieved all known locations of Whimbrels from interior Alaska through a literature review and personal communication with ornithologists working in interior Alaska. I then performed a geographic information system (GIS)-based analysis of known locations to predict other potential breeding areas and crews surveyed these predicted areas to assess the occurrence of Whimbrels. Field crews also characterized multiple habitat features (e.g., slope, elevation, land cover) and I used these in an explanatory model that evaluated factors important to the occurrence of Whimbrels detected on field surveys. To further help me assess the occurrence of Whimbrels crews recorded the presence of potential predators (Skeel & Mallory 1996).

2.3 METHODS

2.3.1 Study area

My study occurred in ‘interior’ Alaska (Fig. 2.1), an area bounded on the east by the U.S.-Canadian border, on the north and south by the continental divides of the Brooks and Alaska Ranges, on the west by the Nulato Hills, and on the southwest by the downstream limits of continuous boreal forest of the Yukon and Kuskokwim Rivers (Gibson 2011). Much of this area is a mosaic of vegetation communities dominated by boreal forest, but also including myriad lakes, rivers, and patches of muskeg, scrub, and tundra that have arisen from the interplay of elevation, aspect, permafrost, surface water, and fire (Alaska Shorebird Group 2008).

2.3.2 Survey planning

I began by creating a map of all published and unpublished records I could find of Whimbrel observations from interior Alaska (Table 2.1). I restricted records to the general area described by Gibson (2011) and the period of 1 May–31 July, the breeding season. I entered these records into ArcMap (ver. 10.0; Environmental Systems Research Institute, Redlands, CA) and created a shapefile of known breeding locations and then overlaid this with the National Land Cover Database (NLCD) 2001 for Alaska (<http://www.mrlc.gov>) to determine potential breeding habitats. I selected the NLCD because it is seamless, has an acceptable level of accuracy compared to other options (Selkowitz and Stehman 2011), and has a higher resolution (30-m pixel size) than datasets spanning the entire North American boreal biome (e.g., North American Land Cover; <http://landcover.usgs.gov/nalcms.php>). The intersection of Whimbrel observations with the land cover layer identified the following NLCD-defined habitats used by Whimbrels during the breeding season: dwarf shrub, shrub/scrub, sedge/herbaceous, moss, woody wetlands, and emergent herbaceous wetlands. I then created a simplified composite layer (i.e., ‘Whimbrel habitat’ map) for all pixels depicting these six habitat types.

Upon developing my map of potential Whimbrel habitat, I created a sampling protocol from which observers in the field could assess the presence or absence of Whimbrels and, if birds were detected, to determine their breeding status. Financial and logistical constraints limited field surveys to areas that were road-accessible throughout interior Alaska. For such sites I created a 20-km-wide buffer centered along seasonally accessible highways and improved roads (10-km buffer per side) and clipped the interior-wide Whimbrel habitat layer with this buffer (Fig. 2.1). I then used tools in the ArcGIS Spatial Analyst extension to remove from consideration habitat

patches that were small (i.e., $<1 \text{ km}^2$) and of high perimeter-to-area ratios as Whimbrels were absent or did not nest at patches of such configurations ($n = 6$) in a small study area in north-central interior Alaska (Harwood *et al.* 2016). I buffered major rivers and streams to further refine habitat patches that were accessible to observers on foot. Finally, I created sampling polygons of predicted Whimbrel habitat in which to deploy count point transects and loaded them into handheld GPS units to guide observers in the field.

2.3.3 Field surveys

I scheduled field surveys to occur 10 May–21 June, the period of peak breeding display and nesting of Whimbrels in interior Alaska (Neipert *et al.* 2014; Harwood *et al.* 2016). My original study design called for the random sampling of polygons of likely Whimbrel nesting habitat, but unforeseen issues involving accessibility to roads and survey areas and too few observers precluded a randomized assessment. Given these caveats, my design evolved for three independent crews to selectively target habitat polygons that met the following objectives: (1) ensure latitudinal and longitudinal diversity among surveyed roads, (2) confirm persistence of Whimbrels at previously documented breeding areas, and (3) sample habitats at varying elevations (e.g., lowlands, uplands, alpine). At each chosen polygon, field crews created transects of up to 21 count points with between-point intervals generally of 500 m, noting point locations with a handheld GPS unit. Transects were generally placed across gradients of elevation and slope to assess the possible range of elevations used by Whimbrels. More forested highways precluded access to points more distant ($>500 \text{ m}$) from the road, resulting in shorter transects in such situations. We occasionally surveyed just outside the study area if the route was logistically efficient and included potential Whimbrel habitat. For example, we surveyed along

the Denali Highway, just south of the study area, because it was the shortest route between the Richardson and Parks Highways, each having sampling polygons.

At each count point (250-m radius) crews conducted 10-min surveys and recorded all species detected (Appendix 2.A). For shorebird species (especially attack-mobbing species like Whimbrels; Sordahl 1981) and their potential avian predators we recorded numbers of individuals (including distinguishing between those newly and previously detected), behavior, and likely breeding status; for all other species we recorded just numbers of individuals. We estimated the percentage (to nearest 5%) of snow present, coarsely characterized the range for the number of trees in the count circle (0, 1–25, 26–100, 101–250, >250), and noted evidence of wildfire. We took photos of habitat in the 4 cardinal directions, and occasionally supplemented these with photos of ecotones. For most points we estimated the percentage (to nearest 5%) of up to 4 habitat types within the count circle according to classifications in Kessel (1979); however, we assessed only the dominant habitat type using both the photos and observer's habitat description based on Alaska Landbird Monitoring Survey protocol (ALMS; Handel & Cady 2004) for count points on the Taylor Highway and Nabesna Road. I derived slope and elevation for all points from a GIS-based digital elevation model layer. Crews assessed breeding status through observations of Whimbrels singing or performing courtship displays, defensive behavior, and by locating nests.

2.3.4 Analyses

I used an information-theoretic approach (Burnham & Anderson 2002) and a binomial generalized linear mixed-effects model to evaluate the importance of specific habitat and

avifaunal community features to the probability of occurrence for newly detected Whimbrels on the count points (i.e., those not already observed on adjacent or nearby points). This ensured that the responses (whether Whimbrels were present) between points were independent, given that individual Whimbrels can at times be detected from > one point. First, I simplified the dominant ‘Kessel’ habitat assessments at each point (Fig. 2.2) to forest, shrub, or meadow, to minimize degrees of freedom and better ensure that the models would converge. Secondly, for my assessment of avian predators, I did not include Long-tailed Jaegers *Stercorarius longicaudus* and Short-eared Owls *Asio flammeus* because they are primarily predators of Whimbrel chicks (Skeel & Mallory 1996) and my surveys preceded the chick-rearing period; however, I did regard these two species as attack-mobbing species like Whimbrels (Skeel & Mallory 1996). As I did for Whimbrels, I considered only newly detected individuals of predators in the analysis to maintain independence between points. I ran correlation analyses on all two-way combinations of predictor variables and detected no problematic collinearity (all $r < 0.5$ and all $P > 0.05$). I used an 8:1 ratio of ‘events’ ($n = 31$ points where Whimbrels were newly detected) to predictors considered (Grueber *et al.* 2011) and selected the four most biologically meaningful. These included two continuous predictors (elevation [m], slope [degrees]), one categorical predictor (simplified Kessel habitat), and one binomial predictor (presence/absence of shorebird predators). I included ‘transect’ as a random effect. The reasoning for selecting elevation, slope, and habitat as fixed-effect variables was because these features are readily available as GIS layers. Assuming their demonstrated importance, such availability would be especially useful for incorporation into future predictive models. Further, if detections of Whimbrel predators were indeed correlated with detecting Whimbrels, then additional datasets or surveys (i.e., those not necessarily targeting or recording Whimbrels) may be useful to future predictive models as well.

This resulted in a candidate set of 16 additive models with 0 (Null), 1, 2, 3, and 4 (Full) predictors. Because the number of events was relatively small and I did not want to over-parameterize the models, I did not fit interaction models. I calculated AIC_c (Akaike's Information Criterion, corrected for small sample size) weights for any supported model (i.e., those without uninformative parameters; Arnold 2010) in the candidate set. I summed the model weights ($\sum w_i$) for each variable using the individual weights of those models containing the respective variable. When model-selection uncertainty was high, I model-averaged parameters to generate estimates, their 95% confidence intervals, and relative importance values. I considered model-averaged parameter estimates with 95% confidence intervals that did not overlap zero to be biologically meaningful, and I assessed effect size on a probability scale. The analysis was conducted using Program R.3.2.2 (R Development Core Team 2014) and packages lme4 (Bates *et al.* 2015), MuMIn (Bartón 2014), and AICcmodavg (Mazerolle 2014).

2.4 RESULTS

Lingering snow cover in 2013 (Alaska Climate Research Center 2013) delayed the start of surveys by 2 weeks, after which field crews conducted 279 point counts along 28 transects distributed among the Dalton, Denali, Elliot, Parks, Richardson, Steese, and Taylor Highways between 23 May–20 June 2013 (mean = 10 points per transect; range 2–21; Table 2.2; Fig. 2.1). We detected Whimbrels on 9 (32%) transects and 31 (11%) count points (Table 2.2). We detected birds at three sites (Elliot Highway, Wickersham Dome, Chandalar Shelf) where they had not been previously reported and none along the Taylor and Steese Highways, despite

previously documented presence for the latter. We also located one and two active nests at Chandalar Shelf and Stampede Road, respectively.

Crews characterized avifaunal and coarse habitat features at all points (Table 2.3). Mean elevation was similar at points where Whimbrels were and were not detected, although the range of elevations was ~345 m wider for the latter. Trees were uncommon among all points, except for along the Taylor Highway. On the 257 points with habitat classification information, about half (45–56%) comprised mostly dwarf shrub meadow (Kessel 1979; level IVb), including all plots on which Whimbrel were detected (Fig. 2.2). Shrub mats or thickets (dwarf, low, and medium) were the next most common habitat types. About 5% of the points comprised scattered woodland, typically of black spruce (*Picea mariana*).

Mobbing species co-occurred with Whimbrels at count points more than three times as often (35%) than at points without Whimbrels (10%; Table 2.3). These species included in decreasing frequency of occurrence (and with numbers of points with and without Whimbrels, respectively): American Golden-Plover *Pluvialis dominica* ($n = 5, 9$), Long-tailed Jaeger ($n = 6, 5$), Upland Sandpiper *Bartramia longicauda* ($n = 0, 8$), Short-eared Owl ($n = 1, 3$), Greater Yellowlegs *Tringa melanoleuca* ($n = 1, 0$), and Lesser Yellowlegs *T. flavipes* ($n = 0, 1$). The percentage of points with potential predators of Whimbrel adults and nests was similar for points with (19%) and without (13%) Whimbrels. Among all points, we detected Common Raven *Corvus corax* four times ($n = 22$) as often as Northern Harrier *Circus cyaneus*, the next most encountered avian predator. For count points on which Whimbrels were initially detected, we were seven times more likely to detect conspecifics (includes both newly and previously detected individual

Whimbrels) on one or more of the adjacent points. We recorded only previously detected Whimbrels on 12 points, and on 12 points we detected both newly and previously detected individuals.

None of the mixed-effects models from my candidate set was well supported, as illustrated by the Null model being the top-ranked (i.e., lowest AIC_C value; Table 2.4). Competing models generally showed little separation so I model-averaged parameter estimates across all 16 models in the candidate set to estimate the probability of Whimbrels being detected at a given count point. The 95% confidence intervals for all parameter estimates overlapped zero, suggesting none of the factors were significant in explaining the occurrence of Whimbrels in my study area.

2.5 DISCUSSION

My study assessed the breeding season occurrence of Whimbrels over a vast area of their Alaska breeding range and, while I expanded the number of documented breeding locations, I also failed to detect birds in many areas with superficially similar habitat and in some instances at sites where they had previously been reported. Reasons for this appear rooted in aspects of the species' biology and in the design and conduct of my survey. Ongoing and future efforts to assess the status of Whimbrel populations range-wide will benefit from discussion of these factors.

Although surveys were necessarily restricted to the road system, I still effected broad north-south, and to a lesser extent east-west, deployment of transects within interior Alaska. Despite

such coverage, I detected Whimbrels at only a third of these locations. Thus, my results reinforce the widespread inference that Whimbrels are patchily distributed spatially on the landscape (Wilke & Johnston-González 2010, Harwood *et al.* 2016). Whimbrels may also exhibit temporal patchiness (e.g., interannual variability), as suggested by their absence at some historically occupied areas, although I recognize that this one-year snapshot may not be necessarily reflective of all years, especially in light of the historically late spring. Although this observed distribution might be attributed in part to incomplete sampling in the Interior, such patchiness has been noted elsewhere in Alaska. Extensive field work at Yukon Delta National Wildlife Refuge suggests that Whimbrels are not uniformly distributed there, despite an abundance of seemingly suitable breeding habitat (B. McCaffery, pers. comm.).

Given challenges like patchiness that I and other researchers (e.g., Pirie & Johnston 2012) have faced in surveying Whimbrels, it is important that more efficient survey methods, ideally ones that incorporate reliably predictive attributes, be identified to more accurately assess their occurrence. Unfortunately, the model variables I tested largely failed to explain the species' occurrence in my study area. Nevertheless, for points where crews did detect Whimbrels, they tended to detect them on adjacent points, too. While it is true that individual Whimbrels were at times detected on consecutive points, adjacent points tended to host new individuals. This result adds further evidence that Whimbrels often nest in clusters (Skeel & Mallory 1996; Harwood *et al.* 2016) and that social interaction may be a major determinant in their distribution. If surveyors are primarily interested in Whimbrel occurrence at a relatively coarse geographic scale (with numbers of individuals unimportant), my results suggest that fewer points per transect could be surveyed and the time saved might be more efficiently spent surveying more transects. Improved

efficiency is critical given the limited time window available for surveying Whimbrels, as well as the vast area to cover within interior Alaska.

In addition to clumped nesting and patchiness, my results supported other well-held insights into the breeding ecology of Whimbrels. Whimbrels throughout their range breed in a variety of habitats (Cramp & Simmons 1983, Skeel & Mallory 1996). Such generalist behavior was potentially borne out both in my model where no habitat variables proved important, and by my anecdotal observations of marked differences among some of the occupied sites. For example, although I most commonly observed Whimbrels breeding in or near tussock tundra (dwarf shrub meadow; Fig. 2.2), I also observed them breeding in close proximity to dense low shrub thickets (Fig. 2.3). Observations of such different habitats were particularly noteworthy to me following a multi-year study of a small population of Whimbrels breeding near the Kanuti River (Harwood *et al.* 2016). Our results there also suggested that Whimbrels were tundra generalists in terms of nest-site selection at coarser spatial scales (i.e., 10–400 m), although I acknowledge that Whimbrels may indeed exhibit habitat specificity not revealed in either of my investigations.

If Whimbrels are indeed phenotypically plastic in their selection of nesting habitats, what drives this adaptive capacity to breed in these varied habitats? For interior Alaska, Whimbrels have bred for millennia in an actively disturbed landscape shaped largely by wildland fires. Although tundra-like habitats may be generally resilient to landscape disturbances (e.g., Higuera *et al.* 2011), the degree to which Whimbrels can occupy (or re-occupy) seral patches post-fire likely depends on the severity of the fire, the extent of the burn, vegetative regrowth, and likely the availability and size of unburned inclusions within the burn perimeter. Although there is copious

literature on fire effects on the boreal forest proper (e.g., Kurkowski *et al.* 2008, Johnstone *et al.* 2011, Gauthier *et al.* 2015), understanding how Whimbrels have adapted to this dynamic landscape requires more studies that focus on the persistence of boreal tundra patches and other habitats associated with Whimbrel breeding, like scrub and bogs (Kolden & Abatzoglou 2012). This may be particularly important given that increased fire activity (Kasischke *et al.* 2010) and other changes to Whimbrel breeding habitats associated with climate change are either already occurring or are predicted to occur in interior Alaska (Tape *et al.* 2006 [shrubification], Roach *et al.* 2011 [lake drying]).

The vulnerability of North American (but not specifically Alaskan) Whimbrels due to climate change was recently elevated to ‘critical’ (Galbraith *et al.* 2014), a level superseding the most sensitive described in the U.S. Shorebird Conservation Plan (Brown *et al.* 2001); this elevation included risk to breeding habitat. This risk assessment was one of several reviews used in the most recent evaluation of conservation status for U.S. shorebirds (U.S. Shorebird Conservation Plan Partnership 2016), which classified even Alaska-breeding Whimbrels as warranting ‘high concern.’ Although I acknowledge the potential for accelerated changes to breeding habitats in interior Alaska due to effects of climate change, I also recognize the potential for Whimbrels there to continue to adapt to this dynamic landscape. Further, Whimbrels arguably face most threats throughout their annual life cycle outside the breeding grounds (e.g., habitat loss and degradation, harvest; Wilke & Johnston-González 2010). Thus in terms of management attention for Whimbrels in interior Alaska, I recommend using these clustered breeding populations as sites for more intensive studies, including local population monitoring (e.g., Neipert *et al.* 2014; Harwood *et al.* 2016) and for deploying transmitter technology to study Whimbrel movements

throughout their annual cycle. Such an approach would help assess the relative influence of intra-seasonal components (breeding, migration, non-breeding) to annual survival.

2.6 ACKNOWLEDGEMENTS

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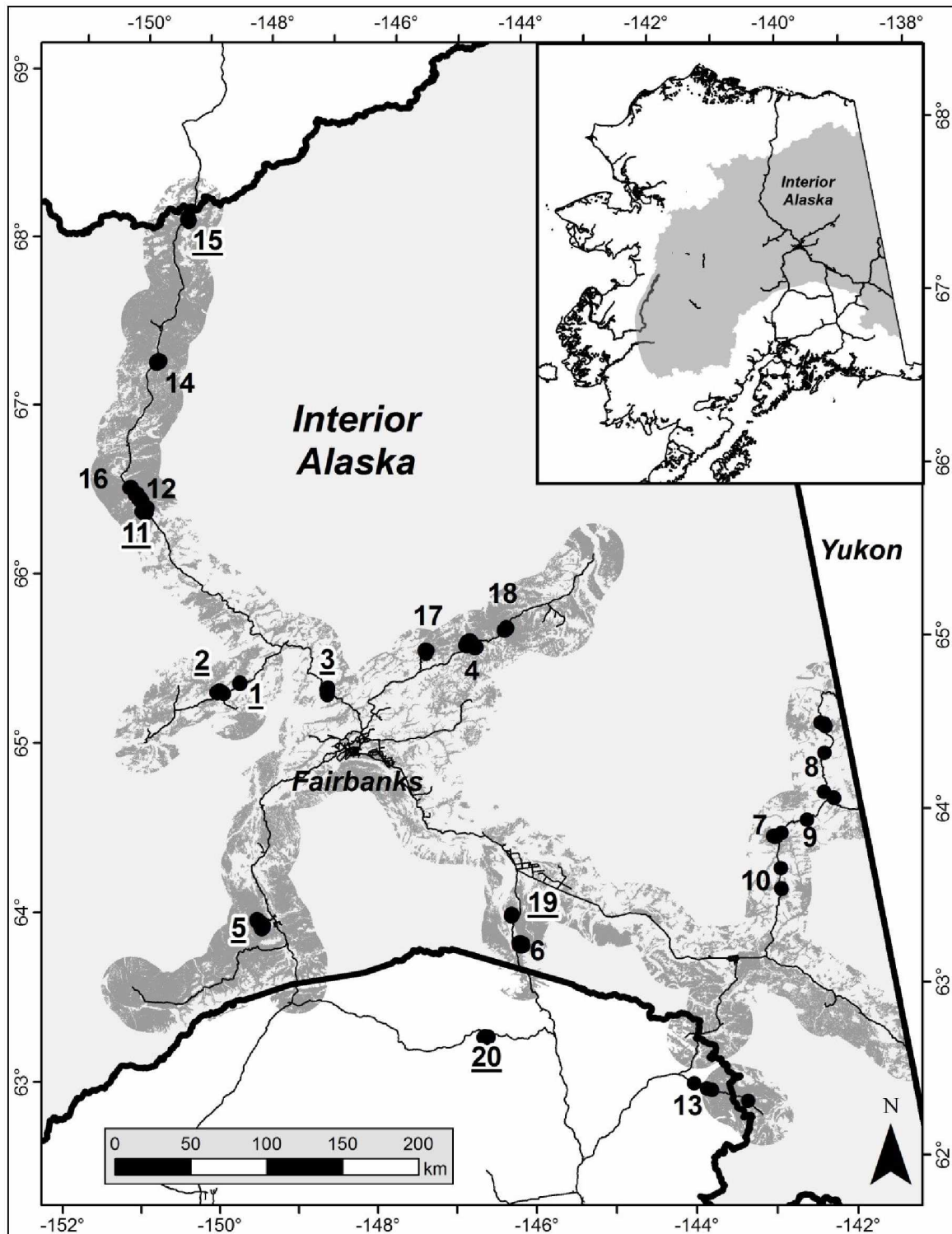


Fig. 2.1. Locations of point count transects (black dots) surveyed within predicted Whimbrel habitat (dark gray buffer) along road system in or near interior Alaska (light gray), 23 May–20 June 2013. Numbers correspond to transects listed in Table 2.2. For transects with Whimbrels, numbers are underlined and have white halo. Inset shows extent of interior Alaska (dark gray) per Gibson (2011). Alaska's road system (black lines) depicted in both maps.

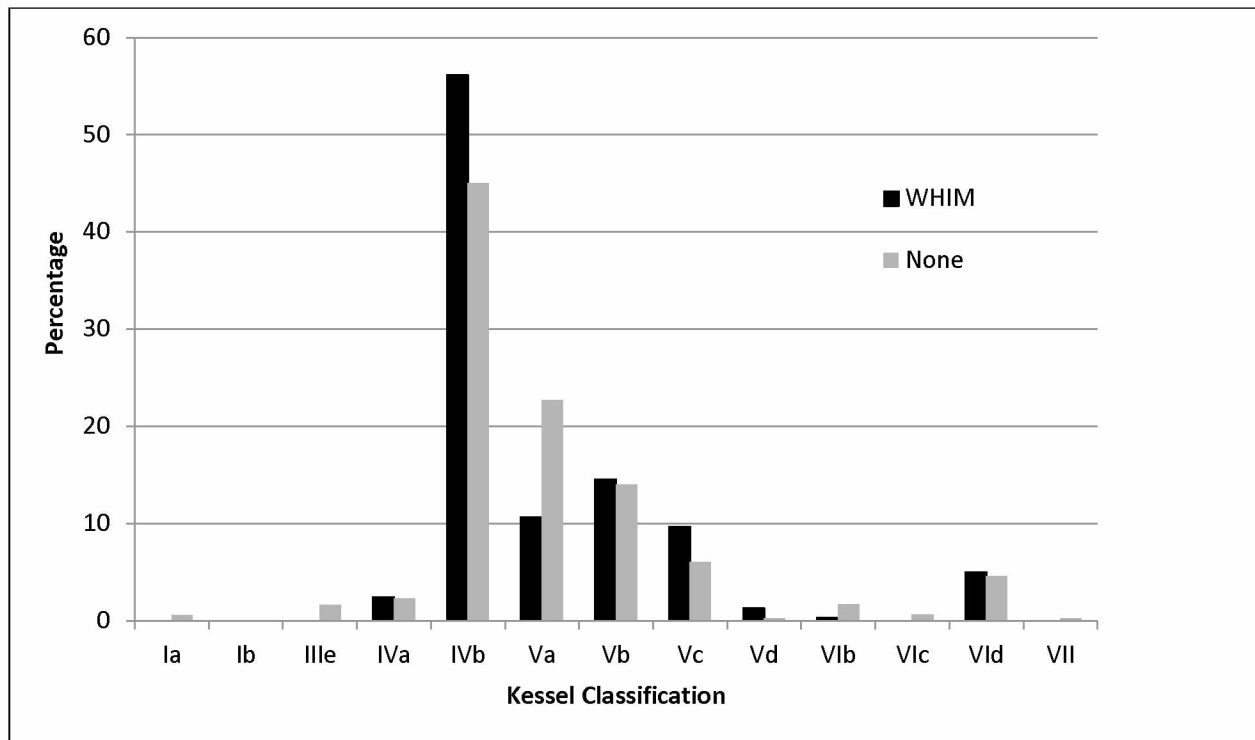


Fig. 2.2. Percentages of habitat types (after Kessel 1979) on count points where Whimbrels were (WHIM; $n = 31$ points) and were not (None; $n = 226$ points) detected in interior Alaska, 23 May–20 June 2013. Classification codes as follows: Ia = lacustrine waters and shorelines, Ib = fluvial waters and shorelines, IIIe = cliffs and block-fields, IVa = wet meadow, IVb = dwarf shrub meadow, Va = dwarf shrub mat, Vb = low shrub thicket, Vc = medium shrub thicket, Vd = tall shrub thicket, VIb = coniferous forest, VIc = mixed deciduous-coniferous forest, VId = scattered woodlands and dwarf forest, VII = artificial habitats. Twenty-two points surveyed along the Taylor Highway and Nabesna Road were omitted from this analysis (see methods).



Fig. 2.3. Photos from count points on Elliot #2 and Donnelly Dome transects where Whimbrels were detected (24 May and 19 June 2016, respectively). Photos capture some of the diversity of occupied Whimbrel habitat observed on the survey, including highly graminoid tussock tundra (top) and low shrub thicket-dominated (bottom).

Table 2.1. Locations in interior Alaska where Whimbrels have been detected during the breeding season (1 May–31 July).

Date	Locality	Status	Reference
12 May 1866	Nulato	NA	Gabrielson & Lincoln 1959
Before 24 July 1903	Circle	NA	Osgood 1909
16 June 1926; regularly since then	Denali National Park & Preserve	Nesting	Dixon 1938, Murie 1963, West 2008; C. McIntyre, unpubl. data
e.g., 19 May 1951	Anaktuvuk Pass	Likely migrants	Irving 1960
2 June 1979; June 2003–09	Firth R./Mancha Cr.	Nesting	Spindler <i>et al.</i> 1980; T. Wild, pers. comm.
30 June 1979; 14 May 2010	Upper Kilolitna River and Torment Creek (Ray Mtns)	Nesting	Matthews 1980; Harwood, unpubl. data
23 May 1981	Solo Lake	NA	Gotthardt <i>et al.</i> 2013
June 1985	Galena	Probable breeding	Gotthardt <i>et al.</i> 2013
e.g., June 1991, June 2013	Denali Highway: Tangle Lakes, Maclaren Valley	Nesting	West 2008; this study
23–24 June 1994; 27–29 June 1995	Upper Cheslina River	Defensive	In Gibson 2011
e.g., June 1995, June 2013	Finger Rock/Caribou Mountain areas	Defensive	West 2008; T. Craig, pers. comm.; this study
2000–2003; 2008–2014	Whimbrel Hill, Donnelly Training Area	Nesting	Gotthardt <i>et al.</i> 2013; Neipert <i>et al.</i> 2014
Pre-2008; 31 May and 21 June 2013	Stampede Road	Nesting	West 2008; this study
June 2003–2009	Coleen River	Displaying	T. Wild, pers. comm.
26 May 2004	Old Stony River	NA	Gotthardt <i>et al.</i> 2013
20 June 2006; 12 June 2010	Innoko NWR	NA	ALMS: Gotthardt <i>et al.</i> 2013
2008–2010	Lake Taiholman, Kanuti R.	Nesting	Harwood <i>et al.</i> 2016
2008–2014	Kanuti Lake, Kanuti R.	Nesting	Harwood <i>et al.</i> 2016
2011–2014	‘Everglades,’ Kanuti R.	Nesting	Harwood <i>et al.</i> 2016
Prior to 2013	Twelvemile Summit	NA	P. Martin, pers. comm.
23–24 May 2013	Elliot Hwy. (16 km NNE and 15.5 km NW of Minto)	Singing	This study
25 May 2013	Wickersham Dome	Unknown	This study
8 June 2013	Chandalar Shelf	Nesting	This study

Table 2.2. Summary of count point transects surveyed for Whimbrels along interior Alaska road system, 23 May–20 June 2013. Shaded cells for Transect ID denote transects on which Whimbrels were detected.

Number on Figure 1	Transect ID	Site Name	Highway	Survey Date	Total count points
1	EL1	Elliot #1 (N of Minto)	Elliot	23 May	18
2	EL2	Elliot #2 (N of Minto)	Elliot	24 May	5
3	WI1	Wickersham Dome #1	Elliot	25 May	4
3	WI2	Wickersham Dome #2	Elliot	25 May	11
4	TM1	Twelvemile Summit #1	Steese	27 May	12
4	TM2	Twelvemile Summit #2	Steese	28 May	20
5	SR1	Stampede Road #1	Parks	31 May	14
6	BCS	Bear Creek South	Richardson	1 June	5
5	SR2	Stampede Road #2	Parks	1 June	21
7	TAM	Taylor Mountain	Taylor	2 June	5
6	BCN	Bear Creek North	Richardson	2 June	5
8	EA1	Eagle #1	Taylor	3 June	7
9	EA2	Eagle #2	Taylor	4 June	2
10	LOG	Log Cabin Creek	Taylor	4 June	3
11	FM1	Finger Mtn. #1	Dalton	5 June	2
12	OM2	Old Man #2	Dalton	5 June	4
13	NAB	Nabesna Road	Glenn	5 June	5
12	OM3	Old Man #3	Dalton	5 June	10
11	FM2	Finger Mtn. #2	Dalton	6 June	20
14	CF1	Coldfoot	Dalton	7 June	20
15	CS1	Chandalar Shelf	Dalton	8 June	15
16	BS1	Beaver Slide	Dalton	9 June	6
12	OM4	Old Man #4	Dalton	5 June	5
17	MP1	Mount Prindle	Steese	12 June	12
4	TM3	Twelvemile Summit #3	Steese	13 June	12
18	ES1	Eagle Summit	Steese	14 June	14
19	DD1	Donnelly Dome	Richardson	19 June	8
20	MS1	Maclaren Summit	Denali	20 June	14

Table 2.3. Habitat measurements (mean, SD, range) and avifaunal features for point counts surveyed along the interior Alaska road system, 23 May–20 June 2013. Percentages are given for the remaining variables.

Variable	WHIM detected (<i>n</i> = 31 points)	WHIM not detected (<i>n</i> = 248 points)
Elevation (m)	853 ± 185 (490–1232)	833 ± 272 (345–1434)
Slope (degrees)	4.6 ± 3.8 0.7–15.1	7.1 ± 5.1 0.0–21.6
Snow present (% of 250-m circle)	2.6 ± 6.8 0–35	6.1 ± 14.6 0–90
Number of trees (modal range)	1–25	0
Evidence of burn (%)	6.5	13.3
Avian predator(s) detected (%)	19.4	12.9
Mobbing species detected (%)	35.5	9.8
Adjacent point(s) with WHIM (%) ¹	83.9	11.7

¹ Whimbrels on adjacent points include both newly and previously detected individuals.

Table 2.4. Model selection results to assess importance of four variables in explaining Whimbrel occurrence at 279 count points along interior Alaska road system, 23 May–20 June 2013. Models are ordered by Akaike’s Information Criterion, corrected for small sample size (AIC_c). K is the number of parameters, ΔAIC_c is the AIC difference from the top model, and -LL is the negative log-likelihood, a measure of deviance. The four variables were (1) elevation (Elev), (2) Slope, (3) Kessel habitat type (Kessel), and (4) presence of avian predators (Preds). Parameter estimates from all 16 candidate models were averaged because of high model uncertainty. No models received greater support than the null model so model weights were not calculated/shown.

Model	K	ΔAIC_c¹	-LL
Null	3	0.00	-48.84
Preds	4	0.24	-47.93
Slope	4	0.90	-48.26
Slope + Preds	5	1.02	-47.29
Elev	4	1.70	-48.66
Elev + Preds	5	1.99	-47.77
Elev + Slope	5	2.00	-47.78
Kessel	5	2.13	-47.84
Elev + Slope + Preds	6	2.17	-46.81
Preds + Kessel	6	2.32	-46.89
Elev + Kessel	6	3.44	-47.45
Slope + Kessel	6	3.46	-47.46
Slope + Preds + Kessel	7	3.56	-46.46
Elev + Preds + Kessel	7	3.70	-46.53
Elev + Slope + Kessel	7	4.20	-46.78
Elev + Slope + Preds + Kessel	8	4.37	-45.80

¹ AIC_c value of the top model is 103.77.

Appendix 2.A. Checklist of birds detected during Whimbrel surveys along the road system in or near interior Alaska, 23 May–20 June 2013.

Greater White-fronted Goose *Anser albifrons*
Canada Goose *Branta canadensis*
Mallard *Anas platyrhynchos*
Northern Shoveler *Anas clypeata*
Northern Pintail *Anas acuta*
Green-winged Teal *Anas crecca*
Greater Scaup *Aythya marila*
Surf Scoter *Melanitta perspicillata*
White-winged Scoter *Melanitta fusca*
Long-tailed Duck *Clangula hyemalis*
Willow Ptarmigan *Lagopus lagopus*
Rock Ptarmigan *Lagopus mutus*
Bald Eagle *Haliaeetus leucocephalus*
Northern Harrier *Circus cyaneus*
Red-tailed Hawk *Buteo jamaicensis*
Golden Eagle *Aquila chrysaetos*
Sandhill Crane *Grus canadensis*
American Golden-Plover *Pluvialis dominica*
Semipalmated Plover *Charadrius semipalmatus*
Solitary Sandpiper *Tringa solitaria*
Greater Yellowlegs *Tringa melanoleuca*
Lesser Yellowlegs *Tringa flavipes*
Upland Sandpiper *Bartramia longicauda*
Whimbrel *Numenius phaeopus*
Surfbird *Aphriza virgata*
Least Sandpiper *Calidris minutilla*
Baird's Sandpiper *Calidris bairdii*
Wilson's Snipe *Gallinago delicata*
Mew Gull *Larus canus*
Herring Gull *Larus argentatus*
Long-tailed Jaeger *Stercorarius longicaudus*
Short-eared Owl *Asio flammeus*
Northern Flicker *Colaptes auratus*
Merlin *Falco columbarius*
Olive-sided Flycatcher *Contopus cooperi*
Western Wood-Pewee *Contopus sordidulus*
Alder Flycatcher *Empidonax alnorum*
Gray Jay *Perisoreus canadensis*
Common Raven *Corvus corax*
Horned Lark *Eremophila alpestris*
Tree Swallow *Tachycineta bicolor*
Violet-green Swallow *Tachycineta thalassina*
Bank Swallow *Riparia riparia*

Appendix 2.A. cont.

Cliff Swallow *Petrochelidon pyrrhonota*
Ruby-crowned Kinglet *Regulus calendula*
Arctic Warbler *Phylloscopus borealis*
Northern Wheatear *Oenanthe oenanthe*
Townsend's Solitaire *Myadestes townsendi*
Gray-cheeked Thrush *Catharus minimus*
Swainson's Thrush *Catharus ustulatus*
Hermit Thrush *Catharus guttatus*
American Robin *Turdus migratorius*
Varied Thrush *Ixoreus naevius*
American Pipit *Anthus rubescens*
Bohemian Waxwing *Bombycilla garrulus*
Lapland Longspur *Calcarius lapponicus*
Smith's Longspur *Calcarius pictus*
Orange-crowned Warbler *Oreothlypis celata*
Yellow Warbler *Setophaga petechia*
Yellow-rumped Warbler *Setophaga coronata*
Wilson's Warbler *Cardellina pusilla*
American Tree Sparrow *Spizella arborea*
Savannah Sparrow *Passerculus sandwichensis*
Fox Sparrow *Passerella iliaca*
Lincoln's Sparrow *Melospiza lincolnii*
White-crowned Sparrow *Zonotrichia leucophrys*
Golden-crowned Sparrow *Zonotrichia atricapilla*
Dark-eyed Junco *Junco hyemalis*
Rusty Blackbird *Euphagus carolinus*
White-winged Crossbill *Loxia leucoptera*
Common Redpoll *Acanthis flammea*

Appendix 2.B. IACUC authorization for Whimbrel surveys along interior Alaska road system, 2013.



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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 23, 2013

To: Abby Powell
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [444764-1] Breeding ecology of Whimbrels

The IACUC reviewed and approved the New Project referenced above by Full Committee Review.

Received: March 18, 2013
Approval Date: April 18, 2013
Initial Approval Date: April 18, 2013
Expiration Date: April 18, 2014

This action is included on the April 18, 2013 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Chapter 3. Intraseason re-use of *Numenius* nest by *Limosa*.¹

Examples of intra- and interspecific re-use of nests abound in the avian world, including eagles enlarging their same nests for many years (e.g., Buehler 2000, Kochert *et al.* 2002) and owls adopting existing hawk and corvid nests (e.g., Artuso *et al.* 2014, Bull & Duncan 1993). Several tree-nesting sandpipers — Green Sandpiper *Tringa ocropus*, Solitary Sandpiper *T. solitaria*, and to a lesser extent, Wood Sandpiper *T. glareola* — even re-use old arboreal passerine nests (Oring 1968). In general, however, intra- and interspecific re-use of wader nests by waders appears to be rare, or at least poorly documented, and the few observations thereof have been largely restricted to between seasons (e.g., Cramp & Simmons 1983 [pp. 521, 531, 582], Hansen 2006; but see Table 1 in Kubelka *et al.* (2014) for a review of interspecific re-use in waders). Such rarity seemingly holds among the tribe Numeniini, as well (e.g., Cramp & Simmons 1983, Dugger & Dugger 2002, Gratto-Trevor 2000, Houston *et al.* 2011, Marks *et al.* 2002, McCaffery & Gill 2001). However, both Cramp & Simmons (1983) and Skeel & Mallory (1996) reported rare intraspecific re-use by Whimbrels *Numenius phaeopus*. Further, Walker *et al.* (2011) observed both rare between-year re-use by Hudsonian Godwits *Limosa haemastica* in Alaska, as well as appropriation of a Short-billed Dowitcher *Limnodromus griseus* nest by godwits in Manitoba. Herein I describe the first documented intraseason re-use of a *N. phaeopus* nest by *L. haemastica* in North America.

On 22 May 2014, I was visiting areas near the Kanuti River on Kanuti National Wildlife Refuge in north-central Alaska, USA, to resight Whimbrels color-flagged in previous years as part of a

¹ Harwood, C.M. 2014. Intraseason re-use of *Numenius* nest by *Limosa*. *Wader Study Group Bulletin* 121(3): 199–200.

five-year breeding ecology study. While in the area, I located a Whimbrel nest (66.15958°N, 151.69716°W) containing one egg. I deemed that the nest had just been initiated based on recent Whimbrel arrival and the phenology of several other nests we had discovered. I flushed the attending bird when I was <50 m from the nest, walked directly to the vacated nest, and recorded its location with a GPS. The attending bird alarm-called regularly while I was near the nest. Its alarm calling attracted its likely mate and a Common Raven *Corvus corax* which it then attack-mobbed, driving it from its territory. Both Whimbrels of the pair were unflagged.

Two weeks later (4 June) I revisited the general area. Expecting to be mobbed by the aforementioned Whimbrels as I entered their territory, I elicited no such response and suspected that the nest had been abandoned or depredated. I approached the nest to confirm its status and at 4 m from the nest flushed a male Hudsonian Godwit instead. The godwit was silent upon flushing and while it perched atop a nearby tree. The former Whimbrel nest now contained two godwit eggs which I believed to represent an incomplete clutch midway through the egg laying period, although I did not float the eggs to infer development stage (Liebezeit *et al.* 2007). I have occasionally observed behavioral dominance by Whimbrels (and never *vice versa*), suggesting that the Hudsonian Godwits likely appropriated an abandoned or depredated nest, rather than usurped it from actively nesting Whimbrels. Given the Whimbrel nest's presumed initiation only two weeks earlier, it was too early to have hatched. As the nesting Whimbrels were not flagged, I cannot confirm if they had departed the study area or were re-nesting elsewhere; however, I did not observe any Whimbrels nesting subsequently within this presumed territory.

The godwit nest was empty upon my next visit on 21 June. As its presumed initiation date was about 3 June, I deemed it was too early to have hatched and thus it had been abandoned or depredated or both. However, I cannot definitively rule out hatching, despite its unlikelihood. The estimated combined laying and incubation period for Hudsonian Godwit is 28 days (Walker *et al.* 2011). Combining this with the unknown failure date for the Whimbrel nest and the similarly unconfirmed development of the godwit eggs, it is possible that the godwit clutch was initiated within a week of 22 May, and that only two eggs had ultimately been laid or there had been partial predation. Nevertheless, I found no evidence of hatching, such as egg shell microfragments (Mabee *et al.* 2006).

In contrast to some 80 Whimbrel nests found in limited tundra areas near the Kanuti River since 2009, I have located only 8 Hudsonian Godwit nests, despite seemingly comparable annual numbers of displaying birds and family groups. With the exception of the nest described here, the microhabitats of these godwit nests have seemingly typified the species, including having considerable overhead cover (Walker *et al.* 2011); however, the sample size is admittedly small. Godwit nests were all located within then moderately to severely burned inclusions of a 2005 wildfire and typically showed much greater overhead cover (e.g., Labrador tea *Ledum decumbens*, dwarf birch *Betula nana*) than the local Whimbrel nests. The re-used nest occurred in a regenerating portion of burned ‘open low mixed shrub-sedge tussock bog’ habitat (Vioreck *et al.* 1992), with three low tussocks *Eriophorum vaginatum* forming a triangle around the scrape, and 20-cm-high Labrador tea interspersed between them. As has been reported for Whimbrel nests in other areas (e.g., Ballantyne & Nol 2011), overhead cover was largely absent.

At Kanuti Lake I have observed Whimbrels and Hudsonian Godwits inhabiting the same tussock bog habitat type, with all located godwit nests occurring within or near presumed Whimbrel nesting territories. While indeed some microhabitat features of their nests seemed to generally differ (e.g., overhead cover), there was nonetheless considerable overlap, including the plant species and microtopography near the nest. The regular use of hummocks or ridges by both species has been documented at Churchill, Manitoba (Skeel & Mallory 1996, Walker *et al.* 2011,). Kubelka *et al.* (2014) recently summarized general hypotheses for interspecific re-use, including energy savings. Given that Hudsonian Godwits create multiple scrapes during a season (Walker *et al.* 2011), this hypothesis seems unlikely in the godwit re-use scenario at hand. Kubelka *et al.* further explored re-use of a Northern Lapwing *Vanellus vanellus* nest by Little Ringed Plovers *Charadrius dubius*. While the authors offered interesting behavioral alternatives for re-use in this mixed-size pair (e.g., lapwing nest served as a supernormal stimulus for courting plovers), they pointed out that most re-use is between more similar species, often when breeding closely. Indeed, such may be the case at Kanuti Lake: Whimbrels and Hudsonian Godwits breed in relative proximity there, with enough overlap in nest microhabitat features that occasionally a nest scrape can be ‘re-used’ not because it is a nest *per se*, but because it simply satisfies the incoming pair’s nest-site selection needs as well.

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General Conclusions

The breeding distribution of Whimbrels has been largely unknown (Skeel & Mallory 1996, Wilke & Johnston-González 2010), despite the value of such knowledge in the management and stewardship of a species of conservation concern. In what is the first dedicated, intensive study of Whimbrels in Alaska, and the first for any shorebird breeding within Alaska's interior boreal forest, I explored where breeding Whimbrels occur, as well as factors influencing their occurrence. I addressed several basic information gaps in the ecology of this poorly studied species as put forth in several conservation plans and status reviews. In Chapter 1, I established baseline metrics for phenology (arrival, initiation, incubation, and hatch), nest density and distribution, nesting habitat characterizations, and nest success for a small population along the Kanuti River in north-central Alaska. In light of projected threats to boreal environments, this included trying to identify factors that may limit Whimbrel distribution and reproductive success within their breeding habitats patchily distributed throughout interior Alaska. I then expanded to a large-scale, regional perspective by surveying Whimbrels more widely across boreal Alaska (Chapter 2) to improve inferences from my local study. During this extensive and intensive study of Whimbrels, I described observations undocumented for the species (Chapter 3) and likely useful for others studying its breeding biology (Appendices A and B).

Many accounts have described Whimbrels as patchily or discontinuously distributed among open-country habitats across the species' breeding range (Cramp & Simmons 1983, Skeel & Mallory 1996) even though access for biologists to the breeding grounds is often challenging and large-scale coverage has not been comprehensive (Wilke & Johnston-González 2010). My

results from both the Kanuti River study area (Chapter 1) and the interior Alaska road system (Chapter 2) support the widespread (but not always tested) patchiness premise: I observed Whimbrels breeding selectively among open tundra-like patches within the boreal forest. Patches not supporting breeding along the Kanuti River (Chapter 1) were smaller (ca. $<1 \text{ km}^2$) and had higher perimeter-to-area ratios (e.g., long, narrow) than breeding sites. Along the road system (Chapter 2), I documented many areas unoccupied by Whimbrels even though these sites were superficially similar to areas where I did observe Whimbrels, suggesting that Whimbrels are not distributed uniformly across the landscape. The landscape of interior Alaska, including near the Kanuti River, comprises a dynamic, wildfire-driven mosaic of habitats in different stages of vegetative succession. To what extent Whimbrels avoid, partly tolerate, or perhaps even exploit open-country patches recovering post-fire is currently unknown; however, differential utility of these seral habitats to breeding Whimbrels over time may in part explain the observed patchiness of Whimbrel occupancy.

Results from both chapters also suggest that some Whimbrels in interior Alaska may either forgo breeding or breed elsewhere in some years. Breeding persisted in all years for only two of the three patches near the Kanuti River (Chapter 1), with the smallest unoccupied in the study's last two years (but was occupied 1993–1995; Kanuti NWR, unpubl. data). Further, numbers of pairs varied annually at the Kanuti Lake site, suggesting that some individuals did not breed there in all years. Indeed, one marked female was seemingly absent for two years before returning to breed, although reduced site fidelity in females is not unexpected (Skeel & Mallory 1996). I observed Whimbrels absent from some historically occupied sites along the road system as well (Chapter 2). With just a one-year snapshot of this larger area, however, I do not know how

commonly non-persistence occurs, or if a historically late spring (Alaska Climate Research Center 2013) can influence whether breeding Whimbrels are present. Given the compressed breeding phenology I observed at the Kanuti River study area, it would make sense if certain breeding sites are not always occupied or that breeding is not necessarily attempted, especially in anomalous years.

My study offers further, albeit limited, support for clustered nesting in Whimbrels (Skeel & Mallory 1996). Cluster analysis suggested clustered nesting for one of four years at one site near the Kanuti River, but not for two years at the other major site (Chapter 1). Although nests were not especially dense relative to the areas I searched, the annual spatial footprints for nests were relatively dense and geographically consistent. I indirectly inferred clustered nesting at occupied sites along the interior road system (Chapter 2) based on the observation of Whimbrels occurring at multiple, often adjacent, points within a given transect. Clustered nesting and a patchy distribution both suggest that social factors may be an important factor in nest-site selection, and likely reproductive success, as enhanced by joint nest and chick defense within the cluster.

I evaluated some dozen habitat features exploring nest-site selection at multiple spatial scales (Chapter 1) and breeding site occupancy (Chapter 2). My results supported other studies where nesting on a hummock (citations in Ballantyne & Nol 2011) and lateral nest concealment (Skeel 1983) were important to nest-site selection at a very proximal scale (0–1 m around nest). More distant features to the nest such as terrain unevenness, complexity in vegetative cover, distance to water, and number of and distance to shrubs (especially medium and tall) and trees were not important features in explaining nest placement. Landscape variables like elevation, slope, and

habitat types likewise failed to explain the presence of Whimbrels more broadly on the landscape. While I acknowledge some limitations such as sample size and study design in my research, I submit that my model results and anecdotal field observations are nevertheless consistent with Whimbrels being open-country habitat generalists in the breeding season; indeed, such phenotypic plasticity in habitat selection has been observed range-wide (Skeel 1983, Grant *et al.* 1992, Pulliainen & Saari 1993, Pirie 2008, Katrínardóttir *et al.* 2015) and may be adaptive. For example, random nest placement may reduce search efficiency in predators and thus improve nest success in White-winged Scoters *Melanitta fusca*, although reduced habitat specificity in this species of conservation concern may also complicate its management (e.g., understanding their distribution and habitat needs; Safine & Lindberg 2008).

Indeed the ecology of Whimbrels on the breeding grounds complicates their management there. Like other researchers have observed elsewhere in the breeding range (Pirie & Johnston 2012), I found detection of Whimbrels (and even access to, once located) in interior Alaska challenging. While surveys along Alaska's road system have direct application to management of Whimbrels found in these most publically accessible areas, it is likely the locations of many small populations beyond these corridors are unknown. Land managers in interior Alaska currently lack appropriate tools to accurately predict Whimbrel occurrence. Although active pursuit of developing Alaska's Interior (e.g., 'Road to Resources' program; Northern Alaska Environmental Center 2016) has stalled in recent years, Whimbrels in the Interior likely occupy areas of keen development interests, including subalpine sites with known mineral deposits. I thus recommend additional efforts to better elucidate any specificity in habitats (including post-fire) and avifaunal community structure that can improve modeling Whimbrel distribution so that

land managers better understand how, where, and when interior Whimbrels occupy the landscape. In Chapters 1 and 2, I identified several sites historically occupied by Whimbrels that have sufficiently large populations and favorable logistics to continue or initiate such research. Although Whimbrels appear well adapted to this ecosystem, understanding better the possible metapopulation dynamics, including local extinctions, recolonization, and habitat continuity (Hanski & Gilpin 1997, Moilanen & Hanski 1998, Hanski 1999) at play with this patchily distributed population would improve local management on the breeding grounds. Clustered birds facilitate opportunities to deploy transmitter technology to understand Whimbrel ecology outside the breeding grounds, where arguably the most serious conservation threats occur (Wilke & Johnston-González 2010).

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Appendix A.

Resightings of marked Whimbrels in Kanuti River study area.

Sixty adult Whimbrels were fitted with a uniquely colored and numbered flag on the upper left leg and a USGS metal band on the upper right during 2009–2012, including 38, 21, and 1 from the Kanuti Lake, Everglades, and Lake Taiholman Study Areas, respectively (Table A-1).

Detection rates for resighting birds one year after marking varied from 47–70%, but decreased over subsequent years. Propensity for nesting for returning birds reached a high of 81% in 2012 which was also the year with the greatest number of birds resighted. One female returned and nested in ≥ 4 yr, 2 males returned in ≥ 3 yr, including confirmed nesting in ≥ 2 . Five males and 1 female returned for ≥ 2 yr, while 21 males and 7 females were resighted in ≥ 1 yr.

Table A-1. Annual rates for resighting previous years' cohorts of flagged adult Whimbrels by sex¹. Fractions represent how many of the observed returning birds nested, Kanuti National Wildlife Refuge, Alaska, 2009–2014.

	2009	2010	2011	2012	2014
2009	21 flagged (13 m, 8 f)	3/7 m 3/3 f	0/0 m 1/1 f	0/0 m 1/2 f	0/0 m 1/1 f
% of flagged returned	(20 KL, 1 LT) ²	47 %	5 %	10 %	5 %
2010		12 flagged (8 m, 4 f)	2/5 m 0/1 f	3/3 m 2/2 f	?/2 m 1/1 f
% of flagged returned		(12 KL)	50 %	42%	25%
2011			20 flagged (13 m, 7 f)	8/11 m 3/3 f	≥1/3 m 0/0 f
% of flagged returned			(16 EV, 4 KL)	70 %	15 %
2012				7 flagged (6 m, 1 f)	4/4 m 0/0 f
% of flagged returned				(5 EV, 2 KL)	57 %
Year's total nesting of returning Whimbrels		6/10 (60%)	3/7 (43%)	17/21 (81%)	≥7/11 (64%)

¹ m = male, f = female

² KL, LT, and EV denote Kanuti Lake, Lake Taiholman, and Everglades Study Areas, respectively.

Appendix B.

Relationship between egg float angles and embryonic stage for Whimbrels.

To estimate date to hatch for Whimbrel nests, I used calculations associated with the egg flotation method most recently described for Alaska shorebirds (Liebezeit *et al.* 2007). The Arctic Shorebird Demographics Network (ASDN; see most recently Brown *et al.* 2014) used these calculations to compose species-specific tables that describe the estimated days to hatch associated with angles observed for both ‘sinking’ (i.e., eggs not breaking water’s surface) and ‘floating’ eggs (i.e., eggs breaking surface). Because there are no published tables assessing the relationship between embryonic stage and flotation angles for Whimbrel eggs specifically, I used the estimations for ‘other shorebirds’ (Tables B-1 and B-2) as advised by the ASDN.

I found considerable concordance between the estimated embryonic development (and thus, projected hatch dates) for float angle calculations derived for ‘other shorebirds’ and the local Whimbrels. I observed hatch for 23 nests for which I floated eggs; 96% of projected hatch dates were within 2 days of observed hatch (mean = -0.087, SD = 2). Non-concordance ranged from projections that were 3 days early to 2 days late.

I estimated 33% of initiation dates (23 of 70) from nests found during laying, while nearly half (34) were estimated by backdating from observed hatch dates. Hatch showed similar concordance regarding synchrony and extreme dates. I derived 61% (43 of 70) of hatch dates from actual observation of hatch, while the remainder was largely split between projecting from known initiation dates and float angle calculations, respectively.

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Table B-1. Relationship between angle of *sinking* eggs and percentage of incubation complete for ‘other shorebirds’ (from Brown *et al.* 2014).

Sinking Eggs	
Angle (degrees)	% of incubation complete
21	0.016
25	0.075
30	0.118
35	0.145
40	0.166
45	0.184
50	0.200
55	0.216
60	0.232
65	0.248
70	0.266
75	0.287
80	0.314
85	0.356
89	0.448

Table B-2. Relationship between angle (90°, 80°, 70°, left to right) of *floating* eggs, including height above surface, and percentage of incubation complete for ‘other shorebirds’ (from Brown *et al.* 2014).

Floating Eggs					
Eggs floating at 90-degree angle		Eggs floating at 80-degree angle		Eggs floating at 70-degree angle	
Height of egg above surface (mm)	% of incubation complete	Height of egg above surface (mm)	% of incubation complete	Height of egg above surface (mm)	% of incubation complete
0	0.42	0	0.46	0	0.50
1	0.48	1	0.53	1	0.57
2	0.55	2	0.59	2	0.63
3	0.62	3	0.66	3	0.70
4	0.68	4	0.73	4	0.77
5	0.75	5	0.79	5	0.84
6	0.82	6	0.86	6	0.90
7	0.89	7	0.93	7	0.97
8	0.95	8	0.99	-	-